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PACIFIC INSULAR FLORAS AND PACIFIC PALEOGEOGRAPHY[1]

PROFESSOR WILLIAM ALBERT SETCHELL
UNIVERSITY OF CALIFORNIA

INSULAR floras were barely touched upon by von Humboldt and other early plant geographers, but interested Charles Darwin particularly as to that of the Galapagos Islands during the voyage of the *Beagle*, 1831 to 1836. In 1859, in "The Origin of Species," he brought forward three ideas concerning them: (1) The species of all kinds which inhabit oceanic islands are few in number compared with those on equal continental areas; (2) although the species are few in number, the proportion of endemic species is often extremely large, and (3) the proportional numbers of the different orders are very different from what they are elsewhere (certain whole groups which might perhaps be expected may be absent). Darwin thus opened the study and discussion of "insular floras" and introduced, although vaguely, their relation to paleogeography.

J. D. Hooker, in 1846, began an enumeration of Darwin's Galapagos plants and, in 1847, followed this by a comparison with the vegetation of some other tropical islands and that of the continent of America. It was in 1867, however, that he delivered his classical lecture on "Insular Floras" before the British Association for the Advancement of Science.

It was Alfred Russel Wallace who, in 1869, first brought forward a clear distinction between oceanic and

[1] Delivered before the seminar on paleogeography in memory of the late Professor W. D. Matthew, University of California, April 22, 1931.

continental islands in his "Malay Archipelago" and in 1880, in his "Island Life," and foreshadowed the connection with geological relations. Grisebach, in 1865, treated of the distribution of floras in the West Indies, and William Botting Hemsley, in 1885, in the publications of the Challenger Expedition, summarized the "Present State of Knowledge of the Various Insular Floras." Hemsley segregated them into 3 categories: (1) Those containing a large endemic element, including endemic genera the nearest affinities of which are not to be found in any one continent; (2) those containing a small (chiefly specific) endemic element, the derivation of which is easily traced, and (3) those containing no endemic elements. Group 1 includes St. Helena, the Juan Fernandez, Sandwich, Galapagos and Seychelles groups; group 2, Bermuda, the Azores, Ascension, the Antarctic islands (including southern Indian Ocean groups); group 3 includes the Cocos Keeling and the low coral groups in various parts of the Pacific.

Coming to a consideration of the floras of the Pacific oceanic islands, H. B. Guppy naturally comes first. In 1906, in the second volume of his "Observations of a Naturalist in the Pacific Ocean," with "Plant Dispersal" as the particular title of the volume, Guppy has shown himself to be one of the most thoroughgoing students of Pacific floras, not only taxonomically and statistically, but in the matter of investigation of the various devices and agencies for dispersal, his opinions being based upon first-hand observations and experiment at various places, both in the Indo-Pacific area and elsewhere, as well as extending over a number of years. His observations have not always been given the careful attention they deserve and, in spite of the positive evidence as to dispersal methods and possibilities, reinforced by numerous undoubted cases he brings forward, later writers have dismissed the possibilities of wide dispersal, even of seemingly promising germules, lightly and, apparently without proper inquiry into the positive trend of the facts brought out by Guppy, as insufficient and have turned to

the much less demonstrable and much more vague hypotheses of land connections, without inquiring any too closely into the possible and probable uncertainties of plant dispersal over such hypothetical land connections. Those interested in the formidable mass of data brought forward by Guppy may be referred to his various volumes.

Guppy outlines the progress of stocking the islands of the Pacific in a certain order, briefly indicated as follows: (1) The age of ferns, and (2) the age of flowering plants (or perhaps better, of seed plants). The latter is again divided into (1) the era of the endemic genera; and (2) the era of the non-endemic genera. The era of the endemic genera is divided into (1) the age of arborescent *Compositae* and (2) the age of the arborescent *Lobeliaceae*. Both of these Guppy considers as belonging to an old Pacific flora, an idea dating back to Bentham (1873) for the *Compositae*. There seems to be suggested, in view of the relationships between the woody Composites and Lobeliads, of peculiar life- or growth-form (the rosette or tufted type) and those of various other insular floras, as well as Andine, E. African and Himalayan representatives, a common origin, and if such is to be insisted upon, it would be in high southern latitudes. Likewise, all seem reasonably adapted to bird carriage. There is certainly enough here to consume much over an hour's discussion, but detail must be passed. Turning to Guppy's "Era of Non-endemic Genera of Flowering Plants," he divided them among the arrivals (perhaps better establishment), (1) of the non-endemic genera of mountain plants; (2) of the wide dispersal (and establishment) of the Malayan plants; and finally (3) the arrival and journeyings of the Polynesian and his plants.

Guppy thus laid down an order of arrival (really meaning migration plus establishment) of the various elements of the Polynesian flora, relying upon dispersal agencies and devices for getting his elements into place, but postulating, instead of land bridges, various emergence and submergence of island groups to account for

presence or absence of the various elements as existing at present. Very little of land-bridge supposition enters into Guppy's hypotheses, which concern themselves only with volcanic (or at times calcareous) islands of fair to considerable elevation, nor did he distinguish migration from ecesis or establishment, or appreciate the nature of closed formations and associations.

Douglas Houghton Campbell (1918, 1919 and 1928) calls attention to various resemblances between the Hawaiian flora and those of adjacent continents and argues for a more or less direct land connection with a hypothetical land area to the southwest of Hawaii. His data are statistical, with little other research behind them. The chief argument is, impossibility of migration over 2,000 or more miles of water, reinforced by the author's experience with the *Hepaticae* and the *Hymenophyllaceae.*

Forest B. H. Brown (1921 and 1922) argues for an Isthmian American origin of the Hawaiian flora, at least as to the Dicotyledons, which arrived during two different periods: (1) During the Jurassic-Comanchic-Cretacic submergence of the Central American region; (2) during the Eocene-Oligocene submergence of the same region. Brown visions dispersal of the disturbed Isthmian flora through ocean currents, rafted on Gymnosperm wood, of 16 families with 31 immigrants during the first wave, whose descendants now number 322 species. This, in Brown's opinion, would account for practically all the endemic genera of flowering plants and make the Hawaiian Angiosperm flora one of the most ancient in the world (1921). Later (1926 and 1928), Brown applies the same origin and migration to account for members of the South Pacific *Cornaceae* (*Lautia*).

Skottsberg (1925), comparing the problems of Hawaii and the San Juan Fernandez Islands, takes issue with Brown as to such wholesale American derivation, and to his paper are added Brown's exceptions to Skottsberg's statements and Skottsberg's rebuttal. Skottsberg in his summary emphasizes the following points:

(1) Juan Fernandez and Hawaii, both groups of volcanic islands, are very remote from one another but with common features in their floras (particularly the "old Pacific" and Antarctic types);

(2) It is hardly probable that vegetation has originated on the islands after they had assumed their present shape;

(3) These are young islands and the flora contains many isolated types where isolation seems the result of considerable age and of geographic changes;

(4) It is not likely that high endemism has resulted from an extermination, in all other countries, of all identical species of close ancestors;

(5) There is much evidence in favor of a continental origin for the Juan Fernandez flora; that it existed long before the present islands were formed; and gradually took possession of them during the submergence of their old home;

(6) Part of this flora was derived from the Antarctic continent by way of South America, thus explaining the affinities with New Zealand or Polynesia. This circuit is preferred to the direct land bridges of other authors.

(7) Skottsberg is confident that future investigators will show that the history of the Hawaiian flora is in its principles similar to that of San Juan Fernandez.

(8) The disappearance of the Tertiary Antarctic flora during the Ice Age is of fundamental importance and has been greatly underestimated by plant geographers. No catastrophe of such dimensions and such consequences has ever befallen the Tertiary flora of the Northern Hemisphere.

In general, Skottsberg has, in his treatment and discussion, touched upon the vital points in a way more thorough and more logical than any of the other phytogeographers. It would be profitable, were time allowing, to take up the points raised all along the line. I may barely mention that he discusses "transoceanic migration," but while he allows that there are active and valuable dispersal agencies, he finds few adequate, al-

though he admits possibly wide water dispersal, but small aerial migration, and even of small bird-assisted migration over 500 to 1,000 miles between Chile and Mas-a-tierra, adding that "the greater the distance, the less probable an aerial migration, even of light spores." This rather summary cloture of overseas dispersal, in face of evidence from dust and spore carriage, and especially in the higher atmosphere, is rather astonishing (see particularly Small (1919) as to possibilities of wind dispersal).

Skottsberg gives greater credence to carriage being more effective by the regular ocean currents and refers to the studies of Guppy, but although he outlines very ably the vicissitudes of current-carried germules, he lays too much stress, as it seems to me, on *presence* as indication of migration possibilities, instead of coupling migration chances, which may be as few or as many as he allows, with establishment and persistence of germules once arrived, which is the more critical and consequently, in all probability, the rarer. Presence of a species means migration (shorter or longer) plus establishment and persistence. It seems that the more logical treatment may be to take the two into account; *absence,* for example, may signify impossibility of migration, but it may also signify lack of ability or opportunity for establishment. These hold equally in cases of possibility of land travel as well as of water travel, but the proponents of land bridge hypotheses seem to believe that land travel is a simple matter, possibly true, possibly less simple, however, than over-water travel, at least for similar distances. A paper of Skottsberg's entitled "Remarks on the Flora of the High Hawaiian Volcanoes" (issued in 1930), deals with the poverty of the "Alpine" Hawaiian flora as compared with that of the lowlands and with the hypothesis that it may be at least in part the remnants of an old Hawaiian stock which formerly inhabited former loftier summits now worn down. The cold and dry climate is one of the factors leading to poverty. Skottsberg is of the opinion that the Hawaiian islands had become

isolated long before the present Alpine region existed and if the current ideas as regards long distance transportation of seeds are correct, new plants ought to have arrived from time to time. Thus far he seems logical and consistent. But he goes on to say that "it was much easier for an immigrant to establish itself in the open highlands than in the closed forest" (a statement not in agreement with experience, since undoubtedly, were this true, the native plant associations would themselves be more dense), and "the result would be a lesser degree of endemism in the Alpine than in the lowland floras." He finds that "endemism, however, is rather more strongly pronounced in the Alpine region." He allows that "it is impossible to deny that, on rare occasions, a chance oversea transport resulting in the establishment of an additional species is effected," but, curiously enough, he adds, "but it is equally impossible to make oversea dispersal responsible for the composition of the actual mountain flora in the Hawaiian Islands." He sums up his belief, that "using the Alpine flora of Hawaii as a test, we arrive at the conclusion that the capacity of the regular dispersal agencies to carry seeds across the Pacific and other oceans has been greatly overestimated." While this may be true, Skottsberg's presentation contains many arguments for a much larger overseas dispersal than he seems willing to admit, and, with a more definite idea that even a sparse placing of plants may, nevertheless, represent a tightly closed association, the whole matter may indeed be one of establishment or ecesis, rather than a limiting of migration to the few species which actually did establish themselves and persist, thus proving by their presence the possibilities of migration as well as establishment.

Skottsberg's (1925) discussion of "Isolated Islands and Origin of Species" is most suggestive. He subjects such factors as isolation, change of environment, divergence of an introduced member of a polymorphous species, recombinations of Mendelian factors, change of genotype and ultimately of phenotype, and from exam-

ples from areas where the history of the flora can be traced back for appreciable periods, he finds no warrant for various opinions as to possibility of pronounced evolutionary change, properly concluding that most ideas expressed are paradoxical, and evolutionary change of moment, to be, at present, without explanation. It has been assumed that insular conditions promoted change, but the same arguments apply to changes in any endemic areas, quite as common on continents as on "isolated" islands.

Skottsberg also discusses the relation of the flora of Juan Fernandez to Willis's theory of "Age and Area," but like most botanists at present, rejects the theory that may be expressed simply thus: That if no other factor prevents, the older the species the wider the area it occupies, but other factors, and often not very conspicuous ones, undoubtedly do prevent; so the uncertainties of this idea help little in attempting to solve problems of insular floras. Skottsberg considers Wegener's hypothesis and Pacific floras. He feels that there are many points in favor of a modified theory of continental drift, troublesome land bridges between America and Africa and between Africa and India are disposed of, etc. But, as postulated in detail, distribution in the Pacific islands seems even more difficult to account for than on a hypothesis of permanence of oceans and continental platforms. Wegener considers that the distance between Juan Fernandez and Chile was wider than it is now and that the Juan Fernandez originated as an independent fragment of the sial sphere, covered with sima basalts. Hawaii, also, in Wegener's opinion, represents an independent piece of land and until comparatively recently in geologic time, in a much broader Pacific Ocean than exists at present. To Irmischer was given, however, the examination of the phytogeographical details as to Juan Fernandez. Skottsberg, on the other hand, is disappointed in Irmischer for any answer to Pacific questions, for, says Skottsberg, his "argument is simple: taking the Tertiary polar movements of Wegener for granted, Irmischer

proceeds to examine the fossil floras." "When their otherwise acknowledged age does not fit the hypothetical position of the pole, he simply redates them in a very unceremonious manner and comes to results which no geologist will approve." "If the hypothesis of pole wanderings is accepted, anything can be proved." "But the pole wanderings remain to be demonstrated and the age of fossil-floras is better known than polar journeys."

As a result of this hasty glance at the principal works on Pacific and other insular floras, there stand out prominently several problems: (1) The old Pacific and Antarctic element, whose migration must have been from the south northward, and this has left three main lines of migration at least to be considered—(a) those of the arboreous Composites, (b) those of the arboreous Lobeliads (see Plate 1), and (c) probably also those of the *Dammara* and *Podocarpus* lines of Gymnosperms or "conifers"—all three of which are to be traced northward on the continental masses as well as over the group of Pacific islands (see Plate 1); (2) the Indo-Malayan element, the most numerous element, whose migration must have been from the west, eastward (see Plate 1); (3) small elements of the floras, possibly boreal, possibly American (especially South American) but none seemingly from the northwest; and (4) introduction and establishment by the Polynesian and Melanesians during their wanderings and settlements. Add to these, (5), the migrations of the vascular cryptogams (ferns and lycopods) and the picture is reasonably complete.

Guppy, as well as most others, probably agree that the migration of the ferns, lycopods and other vascular cryptogams may have been in any direction, judging from the lack of endemic genera. But many or most species being more broadly or more narrowly endemic, and wind being the most probable dispersal agency, argues earlier rather than later dispersal when species, now endemic, may have existed elsewhere or at least time given for origin, spread and establishment of these endemic species. On Juan Fernandez is one fern, *Thyrsopteris elegans,*

seeming the sole survivor of a genus wide-spread in Jurassic times. Similar survival of remnants of the Tertiary flora of southwestern Europe on the Canary Islands points to insular protection against obliterating geologic, climatic and biotic changes on the continents and gives some weight to the view that the so-called old Pacific (or Antarctic) element of the Pacific islands may be a survival of a migration from the Tertiary flora of Antarctica.

Guppy's idea seems to be that the migration of the fern elements of the Pacific insular floras was eastward, but that the arborescent Lobeliaceae and Compositae came from South America. He explains the absence of these elements in Fiji, Samoa and Tonga by supposing that these archipelagoes were sunk at the times this dispersal was active or (Guppy, 2: 257) were represented by "only a few rocky islets tenanted perhaps by conifers," during the greater part of the Tertiary period. This he reinforces from his studies of the geology of Viti Levu (1903), the largest of the Fiji islands.

Guppy's suppositions regarding the mountain floras is that they began their migration when the migrations of the arborescent Composites and Lobeliads had ceased or were diminishing and the migration of mountain genera with endemic species, in turn, gradually slowed up, those from the south stopping first, those from the west (Indo-Malaya) and from the east (a very small element from Pacific North America) possibly still continuing. These are only slightly represented in Fiji, possibly, as Guppy suggests, on account of the low altitude of its mountains.

In this connection Guppy refers to the Gymnosperms or "Coniferae" of Fiji (although of the 3 genera only one possesses cones) and suggests that their arrival may have been in Mesozoic times when they became established and persisted during the almost, but not quite, complete submergence assumed for Fiji during the greater part of the Tertiary. They occur nowhere else among Pacific insular floras except on Eua, in the Tonga

group, whence they may readily have migrated in post-Pliocene times.

Then, Guppy comes to the age of the Malayan plants, now occupying the low-level area. This most considerable stocking of the islands at first extended to even eastern Polynesia, then only to western Polynesia, and has finally slowed up, or has probably for the most part stopped, the reasons for suppression being a mystery to Guppy.

Finally, the Polynesian, in his advent and journeys, has introduced various Malayan species and mixed the floras at least of lower levels in his inter-island trips with food and other cargoes.

Guppy's suggestions as to paleogeography are more concrete than those of any other writer and may be summarized much as follows:

Mesozoic: Fiji alone emergent, received its "conifers"—
Early Tertiary: Fiji all but submerged but retaining its "conifers"; early Polynesia emerging, receiving streams of:
(1) Vascular Cryptogams (ferns, etc.) largely from the west
(2) Arborescent Composites (largely from the south)
(3) Arborescent Lobeliads (largely from the south)
(4) Mountain genera (largely non-endemic; mostly from the south)
Cessation of streams 2, 3 and 4.
Later Tertiary: Fiji re-emerging; all Polynesia receiving the Indo-Malayan streams, which gradually cease largely or entirely.
Pleistocene: Inter-island dispersal.
Post Pleistocene: The Polynesian and his influence.

Guppy postulates nothing as regards land bridges over depths, nor does he favor extensive uniting of members of island groups. His chief paleogeographic changes are rise and subsidence of island groups at various times, particularly of Fiji.

Campbell differs with Guppy in regard to origins, particularly of the Composites and Lobeliads, insisting on land bridges to the southwest and possibly to the south for Hawaii, the only island group he discusses.

Forest B. H. Brown's idea concerns chiefly the changes in the isthmian region of the Americas and demands at least Cretaceous, possibly Jurassic age for Hawaii. Few

botanists will agree with the adequacy of Brown's floristic arguments for exclusive American origin of Pacific floras.

Skottsberg's analysis of the floristic and geographical elements is masterly, but it seems to me that he is too narrow in his allowances for migration possibilities. I am, however, inclined to allow much of Guppy's migration arguments, as to their possibility. Skottsberg proposes no definite scheme of paleogeography for the Pacific. He is inclined to favor the view that much that is most peculiar in the floral elements of the Pacific islands is simply remnant, or relict, of the Tertiary flora of the Antarctic Continent, a flora which we know, even though from small evidence, existed, and of whose extent and variety we can only hypothesize, but which must have been most completely exterminated by Pleistocene and later glaciation, having no land connections (seemingly) for migration northwards at that time. This, of course, is in great contrast to the effects on plant migration of the north polar Pleistocene and later glaciation. Such small fractions as had migrated before the glaciation, he assumes are those preserved in Austral regions (such as S. W. and S. E. Australia, New Zealand and Fuegia, as well as the higher portions of islands and of mountains through Africa, Asia, Polynesia and South America). Skottsberg believes that the Juan Fernandez Antarctic element came by way of a land bridge between Graham Land, the Falklands, Fuegia, etc., to Chile. He believes that the history of the Antarctic element in Hawaii will be found to be similar. He believes that both Juan Fernandez and Hawaii are remnants of larger masses. He is not inclined to postulate a mid-Pacific continent.

Believing, as I feel constrained to, after considering all the evidence, that migration is possible over even very considerable breadth of barrier, whether of sea or of land, and that much of *absence* may be explained by difficulties of germules establishing themselves in new lands, as well as feeling assured that much, if not all of the

seeming cessation of migration which so troubled and puzzled Hemsley, Guppy and others, may be explained by the more recent ecologic view of impenetrability of "closed associations," I see no necessity of postulating any fundamental changes from the point of view of the permanence of the Pacific Ocean as such, and the purely volcanic origin, probably in Tertiary times, of the islands existing in it, in much the same position and form as we now find them. They most certainly did not all appear at once. Fiji and other of the southwestern islands may date back to the Mesozoic, but biogeographic evidence does not necessarily point that way.

It may be well in closing to scan the latest paper on the Pacific, *viz.*, the anniversary address of John Walter Gregory, as president of the Geological Society of London, delivered on February 12, 1930, and entitled, "The Geological History of the Pacific Ocean," since it summarizes the various points of view.

Under the first caption, "The Supposed Permanence of the Pacific," Gregory calls attention to the fact that it "is the greatest geographical unit on earth," for example, 10,000 miles wide from New Guinea to Peru as contrasted with the 1,700 miles from Brazil to Liberia of the Atlantic. On account of its seeming unity, it has been claimed to have existed throughout geologic time, a view urged by J. D. Dana as early as 1847 and adopted by many geophysicists, geologists, paleontologists and zoologists. Other authorities, however, have rejected this idea. A Mesozoic continent was advocated by Huxley in 1870. Baur, because of the fauna of the Galapagos, and Haug, from the point of view of geomorphism, claim that it must have been occupied by a continent, which in the latter's view continued until Kainozoic time, even into late Tertiary. F. von Huene and others, including Gregory, accept the Pacific as the oldest ocean, but not its permanence, Gregory having argued, in 1899, that "the Pacific Ocean may have undergone great changes later than the other oceans."

Under the second caption, "Theories of the Origin of the Pacific," Gregory deals rather summarily with the O. Fisher-George Darwin view that its basin is "the hollow made when the moon was torn away from the earth." He objects to the view, encouraged by the opinion of Suess, that it was an ocean in the Trias, was somewhat smaller in the Jurassic Period and has since been continually reduced in area. In rebuttal, he refers to the fact that the views of many biologists and paleontologists have insisted that the distribution of animals can only be explained by the existence of a continent in the Pacific, or of frequent and extensive land-bridges across it.

Gregory's particular statement at the end of this treatment under this caption reads thus (p. lxxv):

> If the Pacific Ocean has been permanent, we should expect clear manifestations of the persistent unity of its fauna, and that it would be surrounded by the remnants of concentric zones of successive geologic systems. It was the evidence of a circum-Pacific Triassic zone which led Suess to his belief in the Triassic Pacific.

Gregory's proposal is to "consider first, as the most direct existing evidence upon the problem, whether the different geological systems are distributed around the Pacific in accordance with this plan."

He passes then to his third caption, the longest and most important, *viz.*: "The Stratigraphy of the Pacific." Under this, Gregory has eight sub-captions and discussions, beginning with "The Pacific Seas in the Cambrian Period," and passing through to "The Kainozoic Period." The discussions are too long and too detailed to be taken up here, but it may be well to glance at such of his diagrams as illustrate his conclusions. There are four of these, *viz.*: (1) The Cambrian Pacific; (2) The Devonian Pacific; (3) The Triassic Period, and (4) The Jurassic Period, all of which must be passed without comment.

In the Cretaceous, Gregory says, the Pacific was apparently arranged much as in the Jurassic, with narrow seas extending east and west. He does not refer to von Ihering's map here, but says that during the Mesozoic there was an increase in the extent and probably in the

depth of the Pacific Seas. Although he does not refer to von Ihering's conception of the Pacific in the Cretaceous, there is much of the same suggestion.

Of the Kainozoic Pacific, Gregory says that the process of extension and deepening went on, although with great interruptions, until about the middle of that era, when wide-spread subsidence converted the various seas into the Pacific Ocean. He does say that in the "Lower Kainozoic extensive areas of land still lay over parts of the Pacific area," and refers to von Ihering's conception of the condition during the Eocene, seemingly adopting his general conception.

Under caption 4, "The Evidence of Biogeography," Gregory discusses some eight lines of such evidence, beginning with a discussion of (1) the factors of distribution. He apparently rejects any effective dispersal, except over land, but he quotes only certain authorities, and then proceeds to discuss:

(2) Biological trans-Pacific coincidences—first in general, and then takes up reptiles and amphibia, etc. I stop to comment only on a few of them. In a subcaption (7), entitled "The Southern Floras," Gregory discusses Andrews's idea that there has been a land migration-route across the southern Pacific, although he acknowledges that Andrews, who is primarily a geologist, objects to that view.

Gregory also takes up "the evidence of parasitology," or the "von Ihering method," dating from 1891, urging the extreme views that development of parasites, with hosts, shows common origin, routes of migration, land bridges, etc.

In several paragraphs under the subcaption (iii), "The Island Life of the Pacific," he reviews the general and many special facts brought forward by various writers, quoting opposing views of both botanists and zoologists, and favors Campbell's conclusions, evidently denying completely any possibility of adequate overseas migration.

Turning then to geophysics and geomorphism, Gregory discusses "Evidence of Coral Islands," and it seems im-

possible to pass such a paragraph in silence. The paragraph may be quoted rather fully:

> Evidence of Coral-Islands. That the Polynesian Platform is a sunken land is a corollary to Darwin's theory of coral-islands. He inferred that a continent once prolonged Melanesia eastwards into the Pacific, and that its sunken mountain-chains supplied the foundations of the coral-islands. . . .
>
> The inconsistency of Darwin's theory with the permanence of ocean-basins led to many attempts to discredit it. But it has been, I think, fully established by the boring at Funafuti, by the physiographic proofs of subsidence, as clearly stated by Prof. W. M. Davis ("The Coral-Reef Problem," Amer. Geogr. Soc., Spec. Publ. no. ix, 1928), by the gravity observations at Jaluit, by the increasing records of early and middle Kainozoic limestones in their foundations, and by the botanical evidence of subsidence of the Marquesas Islands of from 3,000 to 6,000 feet (F. B. H. Brown, "Botanical Evidence Bearing on the Submergence of Land in the Marquesas Islands," Proc. Pan-Pac. Sci. Cong., 1923, vol. ii (1925), p. 1160). . . .
>
> Personally, I adhere to the view that the Pacific coral-islands afford clear evidence of a subsidence amounting to several thousands of feet, involving —with some areas of elevation—the main part of the Pacific occupied by coral-islands. The scanty paleontological evidence indicates that the sinking was mainly in the Upper Kainozoic Era.

Gregory evidently trusts largely to such evidence to prove subsidence and certainly expresses his belief strongly. One may comment as follows:

(1) The evidence of the boring at Funafuti was not held conclusive by the Coral Reef Committee of the Royal Society and the biological studies on reef structure seem to many to point clearly against subsidence. Funafuti, now, seems to be rising, but that is not to the point. Stanley Gardiner, whose lectures on "Coral Reefs and Atolls" (1931) have been delivered and published since Gregory's presidential address was delivered and printed, while judicial and conservative in tone, seems definitely to reject the coral reefs of barrier and atoll types as necessarily indications of subsidence, and particularly as demonstrated by the Funafuti boring (1931, pp. 146, 162).

(2) The physiographic proofs brought forward by Davis may be convincing as to the islands, but not as to the reefs. Davis's drowned valleys, however, seem usually insignificant (as to thousands of feet of subsidence)

or suggest also other explanations. J. Stanley Gardiner has also discussed this matter (1931, pp. 147, 148, 175) and concludes that the evidence of Davis is both too general and too slight.

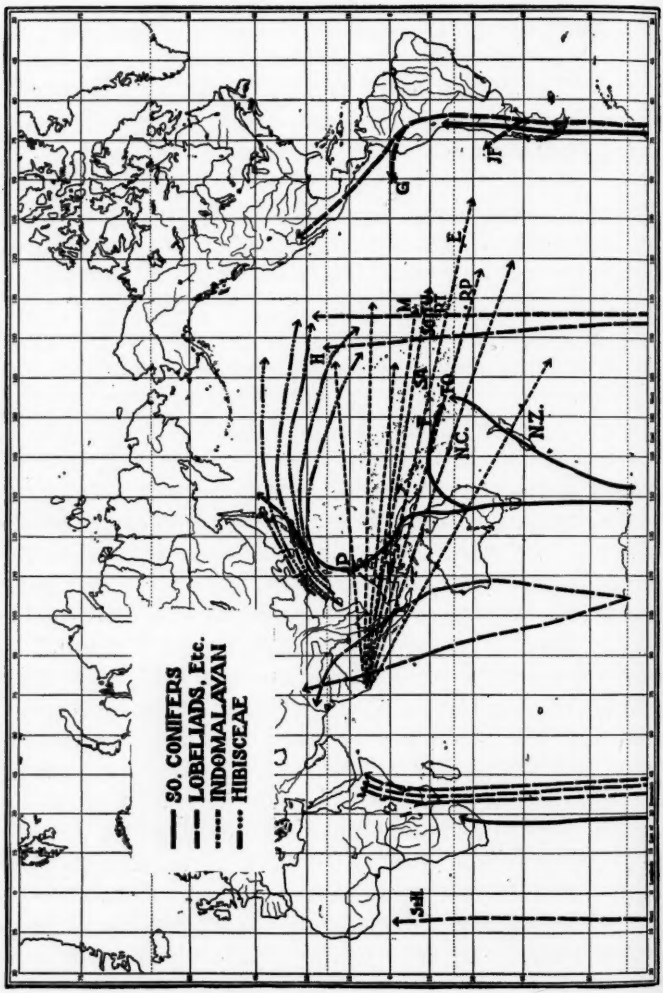
(3) "The gravity observations at Jaluit," and

(4) "The increasing records of Kainozoic limestone in their formations," may be passed over, but paragraph

(5) Relying upon "The botanical evidence of subsidence in the Marquesas, advanced by Forest B. H. Brown" seems almost a botanical joke, since it seems to be the opinion of a man evidently ignorant of altitudinal plant ecology and what might result from subsidence. Mountains on continents show similar differences in altitudinal limits of the same type of vegetation, but subsidence of those showing lower limits is inconceivable.

Proceeding, Gregory turns his attention to matters more of geomorphism and geophysics, which may not be discussed with any authority from the point of view of insular floras.

Finally, in his "General Conclusions," Gregory reiterates the idea "that the Pacific Ocean basin as a whole has not been permanent throughout geologic time; that some parts of it may have been permanent; that the present size is due to a resultant increase in area and depth, for, despite occasional reductions by the upheaval of the floor, subsidence has been the longest and predominant process; that the geological evidence indicates for several periods that the Pacific area was occupied by isolated land-locked seas, which usually had their main extension east and west, and sometimes continued across Asia to Europe, or across America to the Atlantic; that the long Altaid and Alpine mountains . . . were probably continued across the Atlantic and the Pacific by at least raised belts." Gregory believes that these east to west lands across the Pacific were renewed from time to time along different lines, and are due to the heaving of the crust and the corrugations of long bands into fold-mountain systems.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RÉSUMÉ

(1) Insular distribution demands certain streams of migrating ancestors either over long stretches of sea or else over land connections, continuous or only slightly interrupted, but which have, if they existed, left little if any convincing trace.

(2) Geophysicists and geomorphologists incline largely towards the Pacific as a very ancient ocean, the greater part of whose basin has been practically permanent.

(3) Under certain conditions, some geophysicists allow of the possibility of such structures as a mid-Pacific continent or of considerable areas of dry land crossing such a basin.

(4) The majority of paleontologists and biogeographers feel assured that dispersal agencies and devices are totally inadequate for transfer of germules over wide barriers such as oceans. Some allow limited transfer, while a very few feel that migration-limits have been made much more of than allowable, and that establishment after arrival is really the true problem.

(5) Under present relative positions of islands and continents, in order to provide for plant populations now present, immigration must have taken place from all directions, but the principal persistent elements have come from the tropics to the west and the temperate or subtropical regions (present or past) from the south. In other words, the principal streams of migration *plus*

EXPLANATION OF PLATE I

Map of the world, showing possible routes of migration (*plus* establishment) of the principal plant groups now inhabiting the Pacific Islands.

So. "Conifers" includes *Podocarpeae* and *Araucarieae*.

Lobeliads, etc., includes arborescent *Lobeliaceae* and *Compositae*.

Indomalayan includes all relatives of the Indomalayan flora.

Hibisceae includes the peculiar *Hibisceae* of the Hawaiian Islands.

E denotes Easter Island; F, Fiji Islands; G, Galapagos Islands; H, Hawaiian Islands; M, Marquesas Islands; N.C., New Caledonia; N.Z., New Zealand; P., Philippine Islands; R.P., Rapa Island; R T, Rarotonga; S A, Samoan Islands; J F, Juan Fernandez Islands; S O, Society Islands; St. H, Island of St. Helena; T O, Tonga or Friendly Islands; T U, Tuamotu or Low Archipelago.

establishment have been from west to east and from south to north (see Plate 1).

(6) Wind dispersal by the lower planetary winds would be largely from east to west, but cyclonic storms with upward gradient and the upper planetary (reverse) winds may have been even more effective in bringing germules more likely of establishment and persistence.

(7) Bird dispersal may be largely ineffective over wide distances, but examples of occasional (fairly frequent) exception seem demonstrated by definite cases. Such bird dispersal would be most particularly in a north and south direction, as suggested by present extensive bird migration routes.

(8) Current distribution in other directions than by main current drift seems possible on account of reversal and influence of fairly frequent cyclonic winds.

(9) The succession in vegetation from bare ground to climax gradually precludes new elements entering into plant associations and ought to go far towards explaining the seeming cessation of migration of certain groups already established and to preclude the establishing of new immigrants except in disturbed areas (especially where man-made changes occur).

(10) The blotting out of the flora of the Antarctic continent in the Pleistocene has probably removed the source of the old Pacific flora (arborescent Composites, Lobeliads, etc.), but enough remains to indicate, with fair certainty, considerable northward migration before this was accomplished.

(11) My own feeling is that along these lines there are sufficient positive biological cases to outweigh the doubtful ones and to counsel rejection of the negative dispersal arguments for land connections of any considerable magnitude, especially over depths of true oceanic basins, in favor of the positive evidence in favor of such dispersal, which, even if small, is at least *positive,* and to substitute *ecesis* (or establishment) as the practical basis for judgment and further assumption, rather than a discussion of

migration possibilities without correlation with ecesis and persistence, until closed associations slows up and finally brings further penetration to an end (*i.e.*, to an irreducible minimum).

(12) The views of Guppy and of J. Stanley Gardiner, to mention only two biologists who have expressed themselves, seem worthy of deep consideration. From the point of view of insular floras (Guppy, 1906), as well as of coral reefs (largely plant formations) (Gardiner, p. 167) it seems possible of belief that the older idea of the permanence of the Pacific Ocean basin remains possible of assumption and that the various islands and island groups within it are probably volcanic extrusions very little if at all more considerably connected with one another than they are at present. That they appeared largely in late Mesozoic or early to middle Tertiary times and received streams of overseas immigrant germules from all sides of the continental border, certain of which became established to form the present insular floras follows naturally from evidence seemingly firmly established by Guppy and other investigators.

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GENETIC EXPERIMENTS ON HYBRID VIGOR IN MAIZE[1]

PROFESSOR E. W. LINDSTROM
THE IOWA STATE COLLEGE

FROM a theoretical view-point, the genetic nature of hybrid vigor or heterosis is one of the least understood of the major problems in the field of genetics. The dominance of size genes, coupled with linkage in the repulsion phase, is perhaps the best hypothesis, but it needs verification, particularly since it is so difficult to differentiate between the effect of dominance and certain factorial interactions that simulate or obliterate it. Moreover, the recent experiments of Ashby (1930, 1932) on relative growth rate of hybrids and inbred strains have introduced another phase of the problem that requires examination.

The experimental data herein bear directly on these points. The first section of this report deals largely with the skewness of F_2 generations derived from crosses of inbred lines of maize that exhibited marked heterosis. Since no one seems to have recorded individual plant yields (ear weights) in such F_2 generations, the data should be of immediate interest.

The second section is concerned with a direct test of Ashby's hypothesis that heterosis is due to the larger "capital" (greater embryo) with which the F_1 plant starts and not to its higher growth rate.

MATERIAL

All the experimental stocks trace to the standard inbred lines of yellow-dent maize that have been maintained at this station since 1923. At the beginning of this experiment these inbreds had been selfed for seven or more generations. The F_1 crosses had been in yield trials for two years.

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The comparisons between F_1 and F_2 generations in the first section and also the materials for the Ashby test were planned especially for these experiments. The lots were grown in six replicated plots (two rows of 10 hills), planted four seeds to the hill and thinned to three plants, except in the Ashby test, where the seeds were planted one foot apart in the row.

The 1933 season was very favorable for maize. The stand was excellent. The harvested ears were dried to a constant moisture basis in the seed laboratory and there measured. Standard errors, not probable errors, are used in the tables.

I. EXPERIMENTS ON F_1 AND F_2 GENERATIONS INVOLVING HETEROSIS

Three standard, yellow-dent inbreds were used in the crosses:

LAN—12-rowed, long, slender ears, medium season.
LDG—14-rowed, medium-long, medium-sized ears, late season.
OSF—16-rowed, medium-short, medium-sized ears, early to medium season.

Attention was directed only to two F_1 crosses (LAN $\times$ OSF) and (LDG $\times$ OSF) and their F_2 progenies since the third F_1, comprising the two Lancaster inbreds, was thought to be too much influenced by the similarity of these inbreds, and moreover had too many plants with two ears.

In the preceding year, 1932, these two single crosses had averaged 135 per cent. increase in yield over the better parent.

In 1933, the same F_1 crosses plus their F_2 progenies were grown in alternate plots, replicated six times. Ears were harvested only from perfect stand hills. Only first ears were harvested, there being very few with second ears and these were nubbins. In the F_2 lots a small percentage (less than 4 per cent.) of nubbins was harvested, and they are recorded in the F_2 ear weights but were not measured for ear length, diameter and number of kernel rows because of their irregular form.

The F_1 and F_2 curves of individual ear weights (yield) for the two crosses appear in Fig. 1. There is no pro-

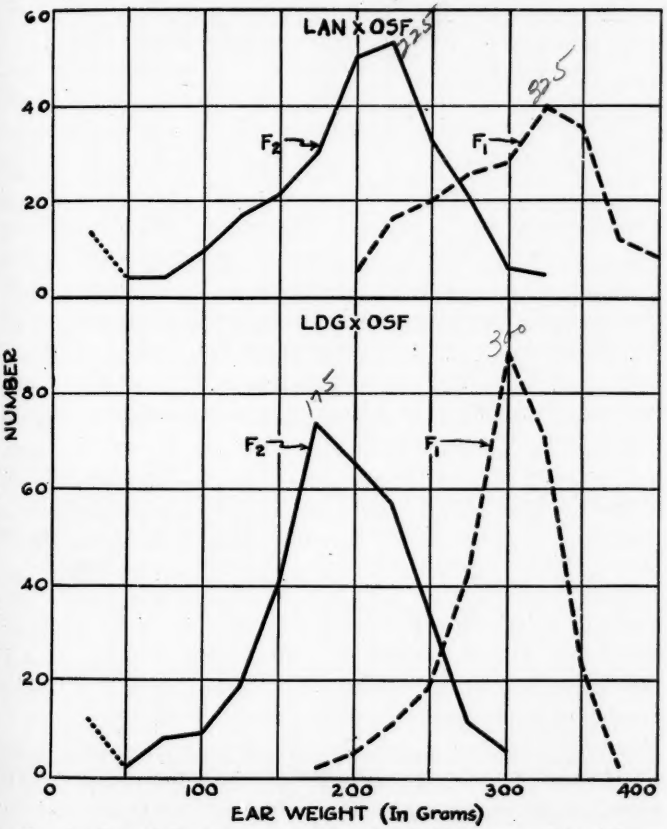

FIG. 1. F_1 and F_2 frequency curves of individual ear weights of two crosses of inbred lines. Dotted portion of F_2 curve represents nubbins.

nounced skewness in either F_2 generation. The third moment g_1 statistic (Fisher, 1932) which measures skewness (zero marks the absence of skewness) shows small negative values of $-.08 \pm .15$ and $-.29 \pm .13$ in F_2 (Table 1). Neither can be considered large enough to indicate any pronounced skewness.

If we call on dominance of size genes to account for the striking F_1 heterosis, we might expect some distinct

TABLE 1

SKEWNESS MEASURES OF TWO F_2 GENERATIONS USING THIRD MOMENT g_1 STATISTIC

Ear characters	F_2 – Lan × Osf	F_2 – Ldg × Osf	Average
Weight	–.08	–.29	–.18
Length	–.93	–.35	–.64
Diameter	–.49	–.03	–.26
Rows	+.39	+.24	+.31
Stand. error g_1	±.15	±.13	±.14

negative skewness in F_2 progenies as the result of such dominance. Of course, such skewness might be dissipated by linkage of good and poor genes in the repulsion phase (Jones, 1917), but it scarcely seems reasonable that linkage could so entirely offset a pronounced dominance of the genes for greater size.

If a large number of genes is involved, the dominance bias would also tend to be obliterated. In addition, any factorial balance between genes having a plus and a minus effect on yield would also modify the skewness.

Direct evidence on this last cause is indicated by an analysis of the component parts of this yield (or ear weight). Measurements of ear length, diameter and number of kernel rows were made for each ear. In Table 1 are the g_1 skewness measures for both F_2 generations. There is striking consistency in both F_2 lots that ear length and to a lesser degree ear diameter show strong negative skewness, whereas number of kernel rows gives positive skewness. Genetically this may be interpreted to mean that there is a dominance of genes for long ears and to a less extent for wide ears, but for kernel rows there is a dominance of genes for smaller number of rows.

For the sake of completeness, the relative differences in the mean values of F_1 and F_2 for the four variables concerned are listed in Table 2. In general these differences corroborate the skewness data, the F_2 values being much smaller than the F_1 except in number of rows where F_1 and F_2 values are more nearly of equal size.

TABLE 2

MEAN VALUES OF F_1 AND F_2 IN THE FOUR MEASURED CHARACTERS

	Cross – Lan × Osf		Cross – Ldg × Osf	
	F_1	F_2	F_1	F_2
Length—cm.	26.1 ± .2	22.4 ± .2	24.7 ± .1	19.9 ± .1
Diameter—mm.	48.1 ± .2	44.2 ± .2	46.4 ± .1	44.1 ± .1
No. rows	14.5 ± .1	13.9 ± .1	16.2 ± .1	16.0 ± .1
Weight—gr.	318.1 ± 3.6	215.2 ± 3.4	310.7 ± 2.2	203.6 ± 2.6

It should be noted that these results are quite opposite to those of Rietz (1927), who found in ordinary distributions of corn ears that "weight showed the tendency to positive skewness whereas the distributions as to lengths of ears were much more nearly symmetrical." He maintains that this is a natural expectancy if volumes (or weights) vary as the cubes of linear dimensions.

Even in our F_1 curves, where genetic variance was at a minimum, there was no evidence of positive skewness. In both F_1 and F_2 the skewness for ear weight was negative. Evidently any natural linear-volume relations in such crosses are overcome by other factors—in this case probably by dominance and the balance of dominant genes for large size and those for small size. If volumes give positive skewness, when diameters are normal, then any negative skewness of weight (as found in our experiments) even though small, could well be interpreted as the result of dominance of large size.

The interrelations between the various ear characters exhibit another angle of the problem. In Table 3, the simple correlation coefficients of these component parts of yield are listed, together with the partial regression coefficients (Betas or path coefficients) and the multiple correlation coefficients, all with ear weight as the dependent variable. Since the multiple correlation coefficients are so high (.919 and .881) there is statistical significance to the results.

Viewing the partial regression coefficients in Table 3, it is evident that both ear length and ear diameter have

TABLE 3

SIMPLE CORRELATIONS, PARTIAL REGRESSION COEFFICIENTS AND MULTIPLE CORRELATIONS OF THE EAR CHARACTERS, LENGTH (L), DIAMETER (D), NUMBER KERNEL ROWS (R) AND WEIGHT (W), IN TWO F_2 GENERATIONS FROM CROSSES OF INBRED LINES OF MAIZE

	F_2 – Lan × Osf	F_2 – Ldg × Osf
Simple correlations (r)		
LD	.385	.204
LR	.099	.003
LW	.798	.772
DR	.562	.591
DW	.727	.573
RW	.326	.243
Multiple correlation (weight as dependent variable)		
$R_{W.LDR}$	.919	.881
Highly significant values of r	.164	.143
Beta partial regression coefficients (ear weight as dependent variable)		
L—Length	$+.606 \pm .028$	$+.680 \pm .027$
D—Diameter	$+.503 \pm .033$	$+.449 \pm .034$
R—Rows	$-.016 \pm .031$	$-.025 \pm .033$

a marked, positive influence on weight, whereas number of kernel rows has a slight negative influence, despite the fact that none of the simple correlations are negative. The consistent nature of both series of F_2 partial regression coefficients may be taken as good evidence of the fact that ear length and diameter influence ear weight in one direction and number of rows in another, an interpretation that is in conformity with that derived from the skewness determinations.

The correlations in Table 3 should be considered as minimum values, since skew distributions tend to produce lower correlation values than would normal distributions. This would also tend to tone down the regression coefficients. For this reason, it is to be expected that the true effects of the positive (length and diameter) and the negative (rows) relations among the partial regression coefficients are really greater than they appear in Table 3.

There is accordingly some direct experimental evidence in favor of the hypothesis of dominance of size genes

as an explanation of heterosis. Whether such a combination of plus and minus effects is a general situation remains to be verified by other investigators with other material. At least with such evidence at hand we need lean less heavily on the linkage of good and poor genes as the only explanation for the normal F_2 curve from vigorous F_1 hybrids.

Empirical experience with prepotency of ear type in topcrosses (Lindstrom, 1931) also substantiates the above deductions. It is consistently noted that certain inbred sires are particularly prepotent in greater ear length, whereas others show a prepotency for fewer rows. In view of the generality of such prepotency, it can not be altogether due to a complementary or "nicking" effect. Prepotency in these cases evidently is the result of a homozygosity of dominant genes in the inbred strains.

The universality of some degree of dominance in the great majority of well-studied genes is a phenomenon that can not be easily dismissed. Dominance of size genes is accordingly a reasonable assumption; and the absence of the expected skewness caused by dominance is not necessarily proof that such dominance is absent.

II. A Test of the Ashby Hypothesis of Heterosis

When in 1930 and again in 1932, Ashby concluded from his experiments that "hybrid vigor in these strains is nothing more than the maintenance of an initial advantage in embryo size" and is not due to a greater efficiency index (relative growth rate) of the hybrid, it challenged the current ideas of heterosis. This was particularly true when he maintained that "the hybrid does not differ in the least from its more vigorous parent as regards relative growth rate and that this relative growth rate is apparently inherited in the manner of a dominant Mendelian factor." Carried to a logical conclusion, this would mean that, in each cross showing heterosis, one particular, major dominant factor was involved, a situation that seems inordinately simple, to say the least. But since his experiments had been repeated with the same results, it seemed

that only experimental considerations and not *a priori* deductions were necessary to test the hypothesis.

Accordingly on June 6, 1933, three standard inbreds (the same as those used in the preceding section), along with the three single F_1 crosses and their three reciprocals were planted in replicated rows. It was planned to reduce the "capital" of the hybrids by the simple procedure of cutting back (above the growing point) the leaves of the young plants, and then to compare their final growth with the untouched inbred parents.

The six F_1 generation progenies were decapitated on four different dates (June 15, 20, 24 and 27) by cutting off approximately from 75 to 85 per cent. (wet weight) of their aerial portions (Table 4). One lot (double decap.) of 18 F_1 plants was cut back on June 15 and again on June 27 when the leaves had grown out again. A second lot (mid decap.) of 18 F_1 plants was cut back once on June 20; and later a third lot (late decap.) on June 24, when the seedlings had from 6 to 8 leaves. Most of the plants recovered from this cutting back, although it made them all slightly later in maturity than the check plants. Notes on silking date and plant height were ascertained (Table 4).

On October 2, the plants were harvested and individual dry weights of the entire plant (cut off at the first node)

TABLE 4

MEAN DATA OF DECAPITATION EXPERIMENT WITH THREE INBRED LINES OF MAIZE AND THEIR F_1 HYBRIDS. PLANTED JUNE 6, 1933. HARVESTED OCTOBER 2, 1933

	Dry weight lbs.		Plant height ft.	Silking date days	No. plants	Per cent. decap.	June dates decap.	Ave. grams removed (wet)
	Whole plant	Ear						
Inbred – Lan	.74	.22	5.8	69.3	10	0	0	0
" – Ldg	.69	.20	6.5	72.0	8	0	0	0
" – Osf	.67	.22	6.0	68.8	10	0	0	0
All F_1 – Check	1.19	.55	8.2	64.6	35	0	0	0
Double-Decap. F_1	.94	.39	7.4	70.6	17	75 + 85	15 + 27	1.7 + 10.6
Mid-Decap. F_1	1.06	.47	8.1	67.3	17	80	20	10.7
Late-Decap. F_1	.86	.37	7.7	67.8	14	82	24	22.7

were obtained from 10 plants each of the three untouched inbred lines, from six plants each of the six untouched F_1 rows and from 48 plants of the three series of decapitations (Table 5.) These were dried in an oven for five days at 160–167° F, and weighed immediately on removal, the ears being also weighed individually.

TABLE 5

MEAN DRY WEIGHT (LBS.) OF WHOLE PLANTS IN INBRED LINES AND RECIPROCAL F_1 HYBRIDS, CONTROLS AND THREE SERIES OF DECAPITATIONS

	Control	Double decap.	Mid decap.	Late decap.	Mean of all decap.
Inbred – Lan	0.74				
Inbred – Osf	0.67				
F_1 – Lan × Osf	1.16	0.97	1.07	0.86	.97 ± .03
F_1 – Osf × Lan	1.13	0.94	0.96	0.74	.87 ± .03
Inbred – Osf	0.67				
Inbred – Ldg	0.69				
F_1 – Ldg × Osf	1.10	0.88	1.04	0.87	.93 ± .02
F_1 – Osf × Ldg	1.13	0.83	0.96	0.79	.86 ± .02
Inbred – Lan	0.74				
Inbred – Ldg	0.69				
F_1 – Lan × Ldg	1.25	0.97	1.06	1.03	1.02 ± .01
F_1 – Ldg × Lan	1.35	1.06	1.29	.....	1.17 ± .06

The mean dry weights, together with other data, are summarized in Table 4, while the individual crosses are given in Table 5, where the reciprocal crosses are listed separately.

The histogram chart in Fig. 2 shows the general results of the experiment clearly. All the three F_1 decapitation series were significantly larger in ear weight and plant weight than the best of the parental stocks. This can only mean that the cut-back F_1 hybrids grew at a faster rate than their untouched parents. Their "capital" had been very appreciably decreased in the early stages of growth, but they overcame the handicap. This was consistently true in every one of the six lots of F_1 hybrids, not only in plant and ear weights but also in plant height.

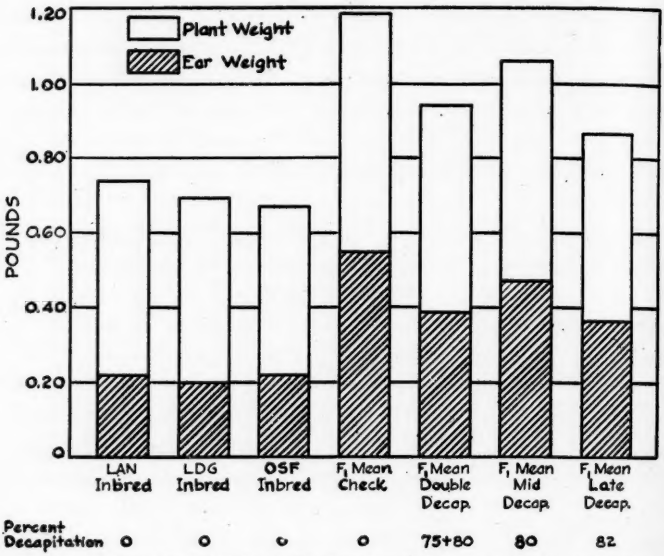

FIG. 2. Mean dry weights of plant and ear of three inbreds, one control F_1 series and three different series of decapitated F_1 plants.

The decapitation served to delay the time of silking to a limited extent, but not enough to be a disturbing factor.

The inconsistency between Ashby's results and the above data may rest in the fact that Ashby's data were gathered from "the grand period of growth," in his case 56 and 83 days from planting in the two experiments, whereas the present experiments involved the entire growth period of the plants, 118 days from planting to harvest. Miller (1931, Fig. 38) found a continuing increase in dry weight of corn in Kansas for a period of 92 days, when his experiments apparently ended. It may well be that the vigorous F_1 hybrid makes its greatest relative growth in plant and ear development at the later stages of its history. At any rate these experiments show that the hybrid has the power to outgrow its better parent even when it is severely handicapped by a reduction of its early "capital" of leaves. That this ability is traceable to a stimulation by wounding is possible but

not probable. The known cases of stimulation by injury are not of the magnitude encountered in these experiments.

In passing it may be noted in Table 5 that slight differences in reciprocal crosses exist. In each of the three sets of such crosses a slight but statistically significant difference is to be found. Ashby noted the same phenomenon. Since the genotype of the embryos of the reciprocals is identical, the cause for such a difference must lie outside the nucleus. Presumably a difference in the endosperm nature could account for the slight superiority of the one hybrid.

Summary

In the first section a biometrical study of the genetic nature of hybrid vigor in maize is reported. From two vigorous F_1 hybrids, data on F_2 yields (individual ear weights) show practically no skewness.

If hybrid vigor is due to dominant size genes, some reason for the absence of F_2 skewness is necessary. The most probable cause is demonstrated by an analysis of the component parts of ear weight. Both ear length and ear diameter show significant negative skewness values, while number of kernel rows shows a positive skewness. Accordingly, the absence of skewness in yield itself may be attributed to a balance of genes, some of which exhibit dominance for large size and some for small size.

The above situation is also indicated by multiple correlation studies of ear length, diameter and kernel rows with ear weight as the dependent variable. The partial regression coefficients (or path coefficients) indicate that both ear length and ear diameter have a high, positive influence on ear weight, whereas number of kernel rows has a slight negative influence. In other words, length and diameter act in one direction and number of rows in another in their effect on ear weight.

In the second section of the paper a specific test of the Ashby hypothesis of the nature of hybrid vigor is pre-

sented. To test the hypothesis that heterosis is due only to the greater "capital" (greater embryo or plant size) with which the hybrid starts in comparison with the parents, six lots of vigorous F_1 progenies were decapitated in the young seedling stages. The aerial parts of the F_1 seedlings above the growing points were cut back so that the hybrids were greatly reduced in their early stages of growth.

Despite this reduction in "capital" all the six F_1 progenies greatly exceeded their untouched parental strains in dry weight of plant and ear, proving that these hybrids must possess a higher growth rate.

It is concluded that hybrid vigor in maize is governed by a number of "size" genes having a marked degree of dominance and producing a higher rate of growth in the hybrid than is found in the parental inbred stocks.

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THE CAUSES OF ASYMMETRIES IN ANIMALS

DR. HANS GRÜNEBERG
DEPARTMENT OF ZOOLOGY, UNIVERSITY COLLEGE, LONDON

INTRODUCTION

THE so-called asymmetry problem in animals has attracted the attention of many students of biology. One can distinguish two different view-points from which this problem can be attacked. The majority of workers have investigated the embryological mechanisms by which in a particular species or group of organisms the formation of asymmetries takes place. This method naturally yields results the validity of which is confined to the group of animals from which the data were obtained. Moreover, such investigations may reveal the mechanism of asymmetry formation, but not necessarily the causes of this mechanism. It is true that many of these workers also have tried to go a step further by elucidating the underlying causes of asymmetry development. Several valuable suggestions about the causes of asymmetries have thus been made. The complexity of the matter, however, renders most generalizations made from the results obtained with single groups unsatisfactory.

In this paper the opposite method will be attempted. By starting from a few well-established facts in the theory of organic development it will be shown which causes and combinations of causes can be expected in asymmetry formation, irrespective of whether these types of causes are realized in nature or not. Thus after having achieved a complete scheme comprising all possible causes of asymmetries one can predict to a certain degree of accuracy the general type of asymmetry which must result from the action or interaction of the different possible causes. Comparison with actual observed asymmetries will then distinguish between mere possibilities and the reality. Further observations will perhaps show that one or another type of asymmetry formation of

which our present knowledge is unable to cite an example, is nevertheless a real way by which asymmetry formation may take place. In any case, the general scheme should be so complete that any type of asymmetry whatsoever should find its place in it.

As mentioned above, many valuable ideas about our problem are scattered throughout the literature. So it would be easy to find predecessors for many or most of the suggestions to be made below. Accordingly, the present author does not lay claim to any rights of priority for this paper, and this may be kept in mind since for the sake of brevity only very few references to previous authors have been included in the text.[1] If, however, this paper diminishes only a little the obscurity which is so wide-spread about the asymmetry problem the author will be quite satisfied.

THE CAUSES OF ASYMMETRIES

As a starting point for our considerations, we may adopt the fact that all organic development is dependent on the complicated interaction of three factors or groups of factors. These are: (1) The genes which are located in the chromosomes; (2) the substratum in which these genes are acting, or, in other words, the cytoplasm; and (3) the environmental conditions under which this reaction between the genes and their substratum, the plasm, takes place. This very general assumption is true for all characters and comprises also asymmetrical organization. For since it is a logical impossibility that any asymmetrical structure could be formed by completely asymmetrical action of the causes, it follows that at least one of the efficient factors (or several) must act in an asymmetrical manner, if differences between the two sides of the body are to result.

[1] A very complete list of references is to be found in the recent monograph of W. Ludwig, "Das Rechts-Links-Problem im Tierreich und beim Menschen," Monogr. aus dem Gesamtgeb. d. Physiologie d. Pflanzen u. d. Tiere, Bd. 27, 1932.

Now let us consider how the three basic factors, genes, plasm and environmental conditions, may act asymmetrically.

In the great majority of cases, the chromosomes and the genes with them are present equally in all the body cells. In some instances, however, exceptions to this rule are to be found; irregularities during the development may cause an abnormal distribution of whole chromosomes or pieces of chromosomes, or mutation in the body cells of the growing organism may result in differences concerning a single gene. Thus both chromosomal and monogenic differences may be asymmetrical.

The physico-chemical conditions of the cytoplasm may be alike on both sides of the body. There may, however, be differences, so that the genes react in a quantitatively or qualitatively different manner with the dissimilar parts of the substratum. In this case apparently the genes act merely as indicators for plasmic differences.

Roughly speaking, the whole body lives under the same environmental conditions. If, however, the individual is in any definite direction to temperature, humidity, etc., gradients during a period which is critical for the determination of a particular organ, the two sides of the body may be influenced differently. This is the case, for instance, for many viviparous forms where the developing embryo is forced to adopt a definite orientation to the nutritive source, by pressure of litter mates and so on. It is also very often met with in the pupae of insects and other temporarily sedentary forms. In all cases such as these the orientation of the developing individual to a gradient is at random so that both sides are equally likely to be influenced. Moreover, if we pass from macroscopic dimensions to another order of magnitude, we may expect that thermodynamic differences (like the Brownian movements) may influence the two sides of the body differently, provided that the developing system is sensitive enough to react to such small differences and that the time which is available for the reaction is too

short to allow the neutralization of one influence by another acting in the opposite direction.

On the other hand, one could imagine that the orientation of the individuals to a gradient is not at random, but that there is a preference for one direction. Finally, environmental influences may be of practically no importance for the determination of the bilateral parts of the body so that these are completely controlled by intrinsic factors, *i.e.*, genes and plasm.

Apparently one and the same symmetrical or asymmetrical organ can be influenced by several of our basic factors at a time. The scheme in Table I shows all possible combinations of their interaction.

TABLE I

Genes or chromosomes	Plasm	Environmental conditions
symmetrical	symmetrical	ineffective
		"at random"
		preferential orientation
	asymmetrical	ineffective
		"at random"
		preferential orientation
asymmetrical	symmetrical	ineffective
		"at random"
		preferential orientation
	asymmetrical	ineffective
		"at random"
		preferential orientation

For practical purposes we can replace this complete scheme by a more simple one. Thus one of the possibilities of Table I never leads to asymmetry formation, where genes are equally distributed through a symmetrical cytoplasm and environmental influences are ineffec-

tive. In addition to this, so far as our present knowledge goes, preferential orientation of animals to an environmental gradient which is not itself caused by intrinsic asymmetries seems not to occur. So we get a simplified scheme.

I. Entirely endogenous asymmetries
  (a) Asymmetries of genes or chromosomes
  (b) Asymmetries of the substratum
II. Entirely exogenous asymmetries (environmental asymmetries)
III. Asymmetries caused by the interaction of intrinsic and extrinsic factors.

The Different Types of Asymmetries

I. Entirely endogenous asymmetries

(*a*) *Chromosomal and genic asymmetries*

In this case either the normal set of chromosomes with which the individual started its development becomes abnormally distributed during the cleavage divisions, or else the original genes undergo mutation in the somatic tissues of the embryo. In either case mosaic formation with all its peculiarities which hardly need to be described here in detail will be the result. Mosaicism of course may or may not lead to asymmetry according to the parts of the body which are built up by the descendants of the cleavage cell in which the chromosomal disarrangement or somatic mutation has taken place. Only those instances of chromosomal or genic differences are to be summarized under this headline in which the process of abnormal distribution of chromosomes or somatic mutation itself is caused by Mendelian genes. Thus it is to be expected that stocks can be obtained in which a certain percentage (up to 100 per cent.) of asymmetrical mosaics regularly occur.

It is a fact well known to geneticists that both types of asymmetries sometimes occur. A few examples may suffice here.

In the case of the silk-worm *Bombyx mori* which has been thoroughly investigated by Goldschmidt and Katsuki in a certain crossbred stock gynandromorphs and

somatic mosaics of the caterpillars (oily versus normal skin) are regularly met with; the characters are independent of each other so that mosaic caterpillars may give rise to gynandromorphs as well as normal imagines, while gynandromorphs may also develop from normal caterpillars. The mosaics are mostly fairly regularly composed of equal right and left halves; sometimes one finds individuals which are halved dorso-ventrally or which exhibit a completely irregular distribution of mosaic areas. The phenomenon as a whole is caused by a gene which is independent of the sex-chromosomes as well as of the chromosome which carries the recessive factor for oily skin; it causes the nucleus of the second polar body to be fertilized by a second sperm so that the organism is derived from two fertilized nuclei.

In the case of *Drosophila simulans* analyzed by Sturtevant there exists a recessive autosomal gene for claret eye-color which results in eggs laid by a female homozygous for this factor having a tendency to eliminate the maternal X-chromosome in early developmental stages. The male parts of the resulting gynandromorphs thus show the recessive sex-linked characters introduced by the father. In addition, the claret gene causes other chromosomal irregularities, particularly of the IVth chromosome.

As an example of a single unstable gene we may cite the miniature-alpha gene in *Drosophila virilis* studied by Demerec which may frequently undergo back-mutation in somatic tissues; thus flies of such a stock may have one normal and one miniature wing, or even a single wing may be composed of normal and miniature parts. The mutability of this gene is stimulated by an independent factor carried in a different chromosome.

(*b*) *Asymmetries of the substratum*

Differences in the substratum with which the genes react are familiar to all students of genetics and experimental embryology. Without such differences we would

be unable to understand why the same set of genes, which is a constituent of all normal body cells, is capable of producing a neural tube in one part of the body and an epidermis in another. All such plasmic differences are epigenetically formed in the developing embryo or in the egg cell before fertilization. Little is known about the causes which underlie this differentiation. All biologists are in agreement that its cause must be an endogenous one. Although a Mendelian analysis of early embryonic stages has hardly been possible as yet it seems quite likely that these plasmic differentiations are also caused by genes. Nevertheless, it seems sure that it is not the *same* genes which at first induce a plasmatic differentiation and then react with it. So it seems justifiable to consider those genes which usually are regarded as being responsible for the appearance of a "character" merely as indicators of a plasmic differentiation which itself has been caused by other genes.

Thus the appearance of any structure in development is dependent on the simultaneous presence of certain genes and the specific substratum with which they react. Conversely, the non-appearance of a character may be caused by the fact that the genes are not capable of reacting with the substratum, or else the latter may be missing (or displaced) while genes which could react are available. Similarly, the place where the reaction takes place is entirely dependent on the localization of the specific substratum, and so the location of a particular structure in the adult individual will be the more constant the more accurately the mechanism of plasmic differentiation is acting in space and time.

All these considerations concern any character and so are valid also for asymmetries. Thus we can expect to find:

(1) Asymmetries which behave as simple Mendelian units when crossed with symmetry. Here the asymmetrical substratum is present in all the individuals of the species, but only some animals contain the specific

gene (or genes) which are capable of reacting with it and which consequently will manifest the asymmetrical character phenotypically.

(2) Asymmetries which are the common characteristic of a whole species or group. Here all the individuals equally are carriers of the asymmetry of the substratum as well as of the specific gene. If there is a particular mechanism which causes the asymmetrical substratum always to be located in the same manner all the individuals of course will show the same type of asymmetry (monostrophy). Environmental influences in some cases may disturb the normal distribution of the substratum and thus cause inversion of the asymmetry; breeding tests, however, will show that such inverted individuals do not inherit their peculiarity because the underlying endogenous causes of plasmatic differentiation have not been altered. If in other instances the location of the substratum is not determined by a particular mechanism but takes place at random we should expect to find a population half of which consists of the R- and half of the L-type of the asymmetry. It is hardly necessary to mention that selection is here incapable of producing pure strains of either type. If, however, in a species showing a monostrophic asymmetry a mutation takes place which alters the specific gene so that it reacts with the substratum of the opposite side a whole inverted population (race, species, genus, etc.) may result. Thus populations may be found which consist of mixed genotypes; here both possible types may be obtained in pure strains by selection. If a cross between them is possible one would expect them to behave as simple Mendelian unit characters.

All those types of asymmetries which one might expect to result from the interaction of an asymmetrical substratum which may or may not react with specific genes in producing the asymmetrical characters of the organism have actually been found to occur in nature.

Asymmetries which arose by mutation in an otherwise symmetrical species and which behave as simple Men-

delian characters allelomorphic to the symmetrical form have been described by Breitenbecher in the pea-beetle *Bruchus quadrimaculatus* (red spots on one, black spots on the other elytron, racemic, limited to the female sex) and by Bridges, by Beliajaff (two rotated abdomens) and by Jollos (unequal wings) in *Drosophila melanogaster*.[2]

Asymmetries which are characteristic of whole species, genera, families and so on are so well known that it is hardly necessary to enumerate the many examples, inasmuch as this recently has been done by W. Ludwig. It may suffice to state that all these different morphological asymmetries found as group characters in Protozoa, trematodes, cestodes, nematodes, echinoderms, snails, crustacea, vertebrates and many others can only be explained by asymmetry of the substratum, since they certainly are caused by endogenous factors and since chromosomal or genic asymmetries lead to entirely different phenotypes, as shown above; moreover, abnormal distribution of chromosomes or somatic mutation are rare exceptions, while normal distribution of the chromosomes and constancy of genes are the rule.

In the majority of cases practically all the individuals of a given species show the same type of asymmetry, thus demonstrating that a particular mechanism is responsible for the localization of the plasmatic differences. This mechanism can be altered or damaged so that inverted individuals result. This has been shown experimentally by several authors for different groups of organisms. In some rare cases even disappearance of the normal asymmetry which becomes replaced by a secondary symmetry has been demonstrated (Ohshima and MacBride in the case of echinoderm larvae). In all species which have been sufficiently investigated the occasional appearance of "spontaneous" inversions has also been observed. From the experimental results we may conclude that in many of such cases uncontrolled environmental

[2] Similar, but less completely analyzed cases are known, *e.g.*, in man; for references see Passqw, 1932.

influences have altered the mechanism which governs the development of the normal plasmatic pattern. In some cases breeding tests have shown that such inverted individuals when crossed together give only normal offspring, which demonstrates that the genotypical basis had not been altered.

On the other hand, as one may learn from Ludwig's monograph, in many of the groups in which one particular type of asymmetry is predominant single species or families occur in which all the individuals show the inverted type of asymmetry if we consider the pattern of the majority of the group as the regular one. This reversal of the asymmetry in whole species or families of course must be a genotypical one. The investigations of Crampton in the snail genus *Partula* seem to show an example in which the process of differentiation of two different asymmetry types is still under way, although this case has not completely been tested genetically. In the case of the fresh-water pulmonate snail *Limnaea peregra,* however, the experiments of Boycott, Diver and co-workers have definitely demonstrated that dextrality and sinistrality are inherited and that these two patterns behave as simple Mendelian units; in order to understand the genetical results it is only necessary to assume that the type of asymmetry for every individual is determined in the egg before fertilization takes place, so that the genes which are contained in the sperm can not manifest themselves before the next generation.

In other cases, no particular mechanism seems to be responsible for the type of asymmetry, so that both possible types occur in equal numbers in a population. This "racemic" behavior is not so seldom met with, while an intermediate type between monostrophic and racemic species ("amphidromic" behavior) seems to occur relatively seldom. Here we must assume that some form of leading mechanism for one of the two possible types is acting but that it is comparatively weak so that it fairly often becomes overwhelmed by counteracting environmental influences.

This short summary of the known facts shows that all the types we may expect really occur in nature and that in several instances it has been demonstrated experimentally that in behavior they correspond to the expectation.

II. ENTIRELY EXOGENOUS ASYMMETRIES

Environmental influences may cause asymmetries in two different ways.

In the first case the environment might act indirectly either by rendering the originally symmetrical distribution of chromosomes or genes asymmetrical or by secondarily influencing the substratum which for a particular organ or structure started as a symmetrical one.

The second way would be by interference with the reaction between the genes and the substratum. Provided this interference were more pronounced on one side than on the other the environmental conditions would here act directly without having previously altered the original symmetry of chromosomes, genes or substratum. In any case either side of the body is equally likely to be influenced so that the population as a whole will be symmetrical. As a measure of this, H. Duncker has introduced an "asymmetry index" the details of which need not be described here. As mentioned in a previous chapter, it is particularly gradients of different kinds which are expected to cause asymmetries. It must be understood, however, that environmental conditions are not necessarily acting from outside the body, since for every cell or organ the neighboring cells or tissues are "external" factors.

As an example of the indirect action of environmental factors one may mention the elimination of entire chromosomes or parts of them which occasionally takes place "spontaneously" during development. Here a chromosome or a piece of it is lost in a cell division, and all the cells which are derived from the incomplete nucleus of course lack the same elements. If these cells are capable of survival a sector is formed which may exhibit a pheno-

typical difference asymmetrically. The size of such a sector is naturally dependent on whether the loss occurred at an early cleavage division or later in development. If the sex-chromosomes are involved gynandromorphs may be produced. Little is known about the actual causes which are efficient in producing such abnormalities of chromosome distribution; the incidence of these usually rare events can, however, be very much increased by the action of x-rays. Whatever the cause of the occasional "spontaneous" cases may be, there is no doubt that they are produced by environmental factors which act either inside or outside the body.

Similarly occasional mutations may take place in somatic cells during the development. These usually do not comprise the germinal tissues and thus are not inherited. If, however, the somatic mutation has occurred very early in the cleavage divisions more or less large parts of the germinal tissues may be altered as well. Thus offspring will be produced which contain the mutated gene in all the body cells. Our knowledge about the external causes of the "spontaneous" somatic mutations is equally incomplete as that of the germinal ones and need not be discussed in detail here.

Little attention has been paid by previous investigators to the possibility that an originally symmetrical *substratum* might be rendered asymmetrical by the action of environmental conditions, either internal or external. In this case the individual would start its development with a symmetrical plasm; during the ontogeny external factors would alter the original plasmatic symmetry; after which the symmetrical set of genes would react either predominantly or exclusively with one side of the body only.

As an example which possibly belongs to this type we may refer to the occasionally occurring cases where one member of a bilateral pair of organs is entirely missing, as is sometimes found in the case of the kidneys in man. Although there is some variation in the size of the kid-

neys there is a wide gap between the smallest examples on the minus side which sometimes occur, and those cases in which the organ is entirely missing. This indicates that the latter cases are caused in a different way. Evidently the Anlage of one kidney was missing; thus there was an asymmetry of the substratum which was caused by environmental conditions, since there is no indication that these cases are caused by hereditary factors.

Another example of this type where the non-genetical basis is better demonstrated is the so-called "half-thorax" in *Drosophila,* where one wing and the corresponding parts of the thorax are more or less completely missing; the result is a very obviously asymmetrically crippled animal, but this anomaly is clearly not inherited.

It may be mentioned in passing that just the opposite process sometimes seems to occur. While in the cases mentioned above the animal started with a symmetrical substratum which later in development was rendered asymmetrical by environmental influences, an individual belonging to an asymmetrical species may get a secondarily symmetrical substratum owing to injuries during its ontogeny. Cases of this kind have been described by MacBride, Ohshima and others in echinoderm larvae which occasionally may have either two coelomata or no coeloma at all. Furthermore, sometimes specimens of usually heterochelous crustacea are found which possess either two large or two small chelae. A third case of this kind has been observed by Boycott, Diver and co-workers in *Limnaea peregra* where individuals rarely occur the shell of which is not coiled at all but is more or less symmetrical like that of *Patella* or *Capulus.* Finally a similar occurrence under natural conditions in *Pleuromamma* has been described by H. Bitynski-Salz.

By far the commonest type of environmental asymmetries is caused directly through the asymmetrical interference of environmental factors with the action of equally distributed genes on a symmetrical substratum. To this type there belong all those well-known smaller

differences between right and left which are usually merely of a quantitative nature. The population if taken as a whole is symmetrical, since influences on the right or left side are equally likely. The single individual, however, may exhibit quite pronounced asymmetries. Since asymmetry of this type has often been dealt with in detail, only a few words about their interpretation may be added.

Some years ago, Ch. Plunkett gave a very careful analysis of the variation of bristles in *Drosophila melanogaster* mutants. He found that the variability of these bristles is due (apart from the main genes) (1) to modifying genes, (2) to external environmental factors and (3) to internal environmental factors. If all the flies are identical for all the modifying factors, the parent-offspring correlation disappears. By keeping the animals under as constant external conditions (temperature, food, etc.) as possible, the correlation between the two sides of the body also approaches zero. Even in this material, however, which was genetically homogeneous and lived under as constant environmental conditions as can be provided in a laboratory there remains a so-called "irreducible variation" where the right and left side of the body vary independently from one another. Plunkett therefore concludes quite correctly that this "irreducible" or "random" variation is caused by factors which influence either one or both or neither side of the body at random. He calls these factors "'random' internal environmental factors," thus distinguishing them from the "external environmental factors." Plunkett is led to this assumption by the fact that this variation still remains among flies living under "identical" external environmental conditions. It seems, however, very difficult to prove that these conditions are really identical for all the flies living in a single culture bottle. Environmental constancy in a strict sense can of course never be reached. It is quite possible that the developing organism is so sensitive that it can respond to gradients of

temperature, humidity, radiation, etc., which are so small that they can not be excluded experimentally. It is, therefore, quite legitimate to assume that it is not an "irreducible variation" under identical external conditions we are dealing with, but an irreducible amount of differences in environmental conditions. This, in the opinion of the author, would avoid the introduction of a new variable which unnecessarily complicates the matter. What we call the irreducible variation of culture conditions may be partially avoided in future under still better standardized breeding methods. It is not impossible, however, that a residue really is "irreducible" as caused by thermodynamic differences. It may be realized, however, as mentioned above, that "external" conditions need not necessarily be located outside the body.

III. INTERACTION OF ENDOGENOUS AND EXOGENOUS CAUSES

Only the interaction of asymmetries of the substratum with external conditions needs to be considered here, since asymmetries of chromosome distribution or of single genes once arisen can never be substantially altered by the subsequent action of environmental conditions.

If an animal which already carries an endogenous asymmetry is influenced by external factors acting equally from all sides, this action may be predominantly or entirely confined to one side of the body only, while the opposite side is less or not at all susceptible to the factors in question. If the basic asymmetry of the substratum is monostrophic, the population as a whole will also be asymmetrical for this environmental alteration. If, however, the original asymmetry shows a racemic distribution, *i.e.*, the population consists of equal numbers of the two corresponding types, then any superimposed externally caused asymmetries would not be distinguishable from asymmetries merely due to irregularities of manifestation; provided it is possible to separate the

individuals according to the r- and l-types of the basic asymmetry, both groups will show that the environmental conditions are more likely to influence one side of the body than the other.

Examples of this kind have been carefully examined statistically by Duncker, Yerkes and others, particularly in flat-fishes and crustacea.

In the flounder *Pleuronectes flesus,* for instance, Duncker found that the number of rays in the pectoral fins is an asymmetrical character. The asymmetry-index in r-individuals is about $+0.6$; its deviation from the value $+1.0$ is caused by the fact that not all the individuals have the higher number of rays on the favored side and that there are still about 36 per cent. of individuals which are symmetrical with respect to the number of fin rays. When investigating l-individuals one finds just the same asymmetry but in a negative direction. If one investigated equal numbers of the two corresponding types together the asymmetry-index would be ± 0. In this example it is so obvious that the character is influenced by the position of the animal on one side that no investigator would even try to treat the animals otherwise except by separating the r- and l-types. If, however, the basic asymmetry were not so obvious and at the same time racemic, a secondary asymmetry caused by the action of environmental influences acting from all sides on an asymmetrical organism could easily be mistaken for a primary entirely exogenous asymmetry caused by gradients to which the animals showed a random orientation.

In those cases in which an asymmetry behaves as a Mendelian unit allelomorphic to the original type a pure asymmetrical stock can be obtained in which all the individuals equally show the asymmetrical character. If the manifestation of such a gene is influenced by environmental conditions a strain homozygous for it may contain a certain percentage of variation in the direction of the normal type. No such case seems to be described as yet.

That injuries in development may occasionally render the substratum of an otherwise asymmetrical species symmetrical has been mentioned in the previous chapter. It may be kept in mind, too, that the environmental inversions in asymmetrical species with monostrophic distribution which have been mentioned in a previous chapter are also caused by the interaction of asymmetries of the substratum with unknown environmental conditions. The same holds true for the behavior of the single individual in a species with racemic distribution; the only difference is that here the mechanism which determines dextrality or sinistrality is so unstable that the environmental conditions are exclusively responsible for, *e.g.*, the direction of coiling of a shell.

The Analysis of Asymmetrical Characters

Having described the possible types of asymmetries one may now take those characteristics which are common to a whole group of asymmetries and may thus serve to distinguish them.

It is likely that this scheme will need correction as our knowledge of other cases progresses. In this connection we lay more stress on the general principles than on the particular cases.

I. Asymmetries of the substratum

Asymmetries which are specific to whole species or races, *i.e.*, found either in every individual or in every individual of one sex of a species or race. Distribution monostrophic, amphidromic or racemic. Environmental inversions give normal offspring only. Genotypical inversions can be isolated as inverted strains which behave as simple Mendelian factors when crossed with the normal type. Asymmetrical races behave in a Mendelian manner when crossed with the symmetrical original type. The asymmetry is always a morphologically well-defined type which is regularly met with.

II. ASYMMETRIES OF CHROMOSOMES AND GENES

Asymmetries which as a rule are characteristic of a race but never of a whole species. Such races behave in a Mendelian manner when crossed with the normal form and show a varying percentage of asymmetrical individuals which are irregular mosaics; these mosaic areas of course are never constant in distribution.

III. ENVIRONMENTAL ASYMMETRIES

General characteristic: selection of a particular type is always ineffective.

(*a*) *Asymmetries due to irregular manifestation*

Asymmetries which in a species or race show continuous variation. Duncker's asymmetry index $= 0$, provided they are not due to primary asymmetries of the substratum with racemic distribution.[3]

In addition to these some occasionally observed asymmetries of a teratological nature which can not yet be separated from the following type to which they possibly belong.

If there existed a kind of asymmetries due to irregular manifestation with a preferential orientation one would expect fluctuating asymmetries with an index $\neq 0$ without any connection with primary asymmetries of the substratum of non-racemic distribution.

(*b*) *Environmental asymmetries of the substratum*

Rare occurrences of a teratological nature, *i.e.*, obviously exceeding the normal range of variation of a particular organ or character. They usually are characterized morphologically by the fact that they either concern an organ as a whole or all those parts of an organ which have a common embryological origin. This type as yet sometimes can not be distinguished from certain other environmental asymmetries.

[3] A deviation from the value 0 is of course only significant if it exceeds three times its standard error.

(*c*) *Environmental asymmetries or chromosomes or genes*

Rare occurrences of a mosaic type. Offspring always symmetrical, usually resembling the normal original form, sometimes showing the peculiarities of the abnormal sector symmetrically on the whole body.

IV. INTERACTION OF ENDOGENOUS AND EXOGENOUS CAUSES

(1) Fluctuating asymmetries usually of a quantitative character present in a species or race. If the primary asymmetry shows a non-racemic distribution Duncker's asymmetry index is $+0$. If the primary asymmetry behaves racemically the index will be 0 if the population is taken as a whole; for either the r- or the l-type it will be $+0$.

(2) Races which contain asymmetrical individuals as well as variation towards the normal; when crossed with the symmetrical original form they behave in a simple Mendelian manner. The asymmetrical character is morphologically well defined in that there is only a simple series of intergradations between asymmetry and symmetry.

As shown above, every asymmetry requires a statistical and morphological investigation as well as breeding tests for a complete analysis. In some cases even a cytological examination will be indispensable.

Summary

A logical system of the possible ways of asymmetry formation is given. A comparison of those possible types with the actual observations shows that most of them are actually met with in nature.

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THE DETERMINATION OF GENETIC CONSTANTS OF RELATIVE GROWTH

M. J. FELDSTEIN AND DR. A. H. HERSH
WESTERN RESERVE UNIVERSITY

INTRODUCTION

HUXLEY (1932) has given an account of the relative growth function, $y = bx^k$, in its application to a wide variety of data from the most diverse organisms from the plant and animal kingdoms, and has discussed the importance which the study of relative growth has for different branches of biology. For the study of relative growth the organism may be considered as a single pattern composed of subordinate patterns, made up in turn of still further subordinate patterns. The difficult problem in this regard is to discover the physiological mechanism by which the whole steers the subordinate parts and how the subordinate ones contribute to the determination of the larger system which they compose. The relative growth function allows a description and comparison of these growth patterns not only in terms of biological units and structures, but it applies also to their description in chemical terms (Huxley, 1932, p. 25 *ff.;* Needham, 1932).

During the course of development and growth the change in size of the organism with the accompanying change in the proportional size of parts masks relationships which are invariant throughout the life history or for relatively long periods, and the character of which is disclosed by the value of the constants of the relative growth function. It is becoming increasingly clear that individuals which differ genetically in regard to modifiers of size, or of number of parts, or of amount of chemical product, differ in regard to these invariant relationships during the course of development and growth. In such cases b and k are genetic constants of relative growth. They give us information in terms of relative

growth on the mode of action of the genetic differences of the original fertilized egg as they intervene in the developmental processes to bring about their characteristic phenotypic effects.

Methods of Determining the Constants of the Relative Growth Function

Since 1924, when Huxley showed that the power function, $y = bx^k$, was a close approximation to the relationships involved in relative growth, the constants for most of the data have been determined mainly by the graphic method. This method is no doubt adequate when the genetic differences are great and when no close comparison is desired. But for an organism where a high degree of genetic control makes it feasible to undertake an estimation of the differences in the constants of relative growth that are brought about by smaller genetic differences, such as a difference in a single chromosome, or in a section of a chromosome, or even in a single gene, it is obvious that the graphic method falls short of the main desideratum, since even experienced workers may not agree on the values of the constants derived from the same data by this method. The method of averages is also faulty.

The time-honored method of least squares is clearly to be preferred. But in the use of this method one is confronted with the problem of deciding whether the best fit should be made with regard to the original arithmetic values of x and y or to the logarithms of these values. A possible relationship suggested by the use of the values of the constants determined by the one method may be obscured by the values determined by the other method. The purpose of the present article is to compare the results obtained by the use of these two ways of applying the method of least squares to the data obtained (Hersh, 1931) in studying the effect on the dorsal and ventral lobes of bar eye of Drosophila as sections of an Xple chromosome were added singly and in various com-

binations to a forked bar X-chromosome supplied by a stock which had been subjected to selection for low facet number by Professor Charles Zeleny.

TWO WAYS OF APPLYING THE LEAST SQUARES METHOD

The two ways of applying the least squares method are defined by the process by which the relative growth function

$$y = bx^k \tag{1}$$

needs to be treated in order to determine the values of the constants. By taking logarithms of both sides, equation 1 becomes

$$\log y = \log b + k \log x \tag{2}$$

which is the familiar form of linear equation with slope k and y-intercept log b.

A least squares solution of equation 2 will not give the same values of b and k as the least squares solution of equation 1. But since in the calculation it is more convenient to start with the function in logarithmic form a least squares solution of equation 1 is readily obtained by applying a proper system of weights to equation 2 (see Camp, 1931, p. 114, and Leland, 1921).

As Leland (p. 136) points out, the precise method of fitting a least squares line to a power or an exponential function requires that (italics in the original) "special attention must be given to the *weights* . . . for the weights of the reduced linear equations will not be the same as before reduction to the linear form. . . . If the weights of the original observations of y_1, y_2, y_3, . . . etc., are w_1, w_2, w_3, . . . etc., the corresponding weights of the function $\log y_1$, $\log y_2$, $\log y_3$, . . . etc., will be $y_1^2 w_1$, $y_2^2 w_2$, $y_3^2 w_3$, . . . etc. Or, if the original weights are equal the reduced equations will be weighted directly as the squares of the corresponding observed values of y'."

Hence, in fitting a least squares line to the equation, $y = bx^k$, by using the logarithmic transformation to the

linear form, and taking into account the theoretical as well as the observed weights, the observation equations become

$$y^2w\ (\log y - \log b - k \log x) = 0 \tag{3}$$

$$\log x\ [y^2w\ (\log y - \log b - k \log x)\ ] = 0 \tag{4}$$

where w is the frequency weight of the given observation equation. The number of observation equations is obviously the same for both sets 3 and 4 and is determined by the number of classes in which the values of the y's are grouped. The normal equations which are solved simultaneously to give the values of k and log b for a given set of data are the sums respectively of the two sets of observation equations. These summands are as follows:

$$\Sigma\, y^2w \log y - \log b\, \Sigma\, y^2w - k\, \Sigma\, y^2w \log x = 0 \tag{5}$$

$$\Sigma\, y^2w \log x \log y - \log b\, \Sigma\, y^2w \log x - k\, \Sigma\, y^2w\ (\log x)^2 = 0 \tag{6}$$

These equations are solved in the usual way for the determination of the values of the constants. But for the sake of a later comparison it can readily be shown that

$$k = \frac{\Sigma\, y^2w\ [\Sigma\, y^2w \log x \log y] - (\Sigma\, y^2w \log x)\ (\Sigma\, y^2w \log y)}{\Sigma\, y^2w\ [\Sigma\, y^2w\ (\log x)^2] - (\Sigma\, y^2w \log x)^2} \tag{7}$$

This equation shows that k is the ratio of two quantities: (1), the difference between the weighted summations of the products of log x and log y and the product of the weighted summations of log x and log y, and (2), the difference between the weighted summation of the squares of log x and the square of the weighted summations of log x.

The method outlined above gives a line fitted by least squares to the equation, $y = bx^k$, when the test is made in terms of the arithmetic values of the reduced original data. The distinctive feature of the method is that each observation equation is given the observed weight w and the weight y^2 which mathematical considerations demand. We may call this method the y^2-weight correction method.

When the individual equations are not given their respective y^2 weights, then the result is a least squares line fitted to equation 2. The method is formally equiva-

lent to the calculation of the ordinary regression line of log y on log x. In this case the normal equations which are solved to obtain the values of k and log b differ from equations 5 and 6 only in regard to the y^2's. Perhaps a shorter method which gives identical results is to calculate k directly from the familiar general formula for the regression coefficient

$$k = r\frac{\sigma \log y}{\sigma \log x} = \frac{N\Sigma \log x \log y - \Sigma \log x \cdot \Sigma \log y}{N\Sigma (\log x)^2 - (\Sigma \log x)^2} \qquad (8)$$

It can readily be seen that formulae 7 and 8 differ merely in the application of the different system of weights. N of equation 8, the number in the population for which the determination is made, is identical to the sum of the observed weights (Σ w) of equation 7. When k is calculated from the regression formula, log b may be readily obtained by substituting in the general equation for the regression line of log y on log x and solving for the value of log y when log x = 0.

By this second method the principle of least squares holds only when logarithms are used, but does not apply if the logarithms are translated into their respective anti-logs. This method differs then from the first one where the principle of least squares applies to the original arithmetic values. We shall refer to it as the regression method.

COMPARISON OF THE RESULTS OF THE TWO METHODS

These two ways of applying the method of least squares were carried out on data of facet number in the dorsal and ventral lobes of bar-eyed *Drosophila melanogaster* in fifteen stocks which differed in regard to the genetic constitution of their X-chromosomes. The constants of the relative growth function for these data determined by the first method were published previously (Hersh, 1931) and are given here in Tables 1 and 2, along with the constants derived by the second method, *i.e.*, the regression method. The constants in the tables calculated by the regression method are designated by Greek letters.

TABLE 1

AVERAGE FACET NUMBER AND THE GENETIC CONSTANTS OF RELATIVE GROWTH FOR FEMALES OF THE FIFTEEN BAR-EYED STOCKS OF DROSOPHILA MELANOGASTER DETERMINED BY THE TWO METHODS

Genetic Constitution	Average facet number	κ	k	log β	log b
sc + + + + + f B	53.9	1.173	1.258	− 0.414	− 0.541
+ ec + + + + f B	63.1	1.573	1.532	− 1.040	− 0.976
+ + cv + + + f B	67.6	1.100	1.036	− 0.284	− 0.177
+ + + ct + + f B	45.1	1.050	0.973	− 0.188	− 0.078
+ + + + v + f B	59.8	1.493	1.324	− 0.964	− 0.690
+ + + + + g f B	47.1	0.920	0.972	− 0.003	− 0.108
+ + + + + + f B	57.2	1.188	1.128	− 0.421	− 0.328
sc ec + + + + f B	56.8	1.139	1.333	− 0.430	− 0.728
sc ec cv + + + f B	67.1	1.505	1.486	− 0.943	− 0.908
sc ec cv ct + + f B	88.7	0.812	0.951	+ 0.196	− 0.037
sc ec cv ct v + f B	86.6	1.085	1.098	− 0.284	− 0.304
sc ec cv ct v g f B	65.5	1.345	1.466	− 0.580	− 0.697
+ + + + v g f B	50.9	1.405	1.422	− 0.673	− 0.434
+ + + ct v g f B	48.2	1.121	1.230	− 0.279	− 0.482
+ + cv ct v g f B	58.5	1.234	1.242	− 0.472	− 0.764

A cursory inspection of these values shows that sometimes κ is larger than k and sometimes it is smaller. The same conclusion holds for the values of log β and log b. But there is a noticeable consistency in that high values of κ are found with the high values of k, and low values of κ with low values of k. It was shown for the values of b and k calculated by the first method (Hersh, 1931) that b is a decreasing exponential function of k, that is:

$$b = B\, e^{-rk} \qquad (9)$$

The values of B and r published in the paper mentioned were determined by the method of averages. Their values computed by least squares are for females, respectively, 1.397 and − 3.519, and for males 1.665 and − 4.376 for log B and r, respectively.

The relative growth constants determined by the regression method likewise conform to the same function. The constants in the above equation are 1.458 and − 3.656

TABLE 2

AVERAGE FACET NUMBER AND THE GENETIC CONSTANTS OF RELATIVE GROWTH FOR MALES OF THE FIFTEEN BAR-EYED STOCKS OF DROSOPHILA MELANOGASTER DETERMINED BY THE TWO METHODS

Genetic Constitution	Average facet number	κ	k	$\log \beta$	log b
sc + + + + + f B	88.5	1.190	1.242	−0.586	−0.674
+ ec + + + + f B	93.2	0.804	0.857	+0.082	−0.010
+ + cv + + + f B	111.5	0.551	0.633	+0.584	+0.438
+ + + ct + + f B	72.3	0.973	0.911	−0.187	−0.078
+ + + + v + f B	106.2	1.078	1.101	−0.443	−0.481
+ + + + + g f B	64.0	0.760	0.998	+0.148	−0.237
+ + + + + + f B	87.8	1.122	1.112	−0.453	−0.432
sc ec + + + + f B	93.6	1.208	1.223	−0.652	−0.677
sc ec cv + + + f B	111.6	0.893	0.940	−0.034	−0.120
sc ec cv ct + + f B	139.9	0.704	0.666	+0.361	+0.435
sc ec cv ct v + f B	145.6	0.640	0.670	+0.486	+0.434
sc ec cv ct v g f B	87.5	0.994	0.787	−0.153	−0.306
+ + + + v g f B	70.9	1.075	1.066	−0.324	+0.086
+ + + ct v g f B	71.9	0.806	0.809	+0.090	+0.485
+ + cv ct v g f B	80.6	0.641	0.603	+0.417	+0.221

for $\log \beta$ and ρ for females, and 1.620 and −4.277 for males.

When the constants are computed by the regression method, the angle between the lines representing the sexes is 2.13°, which compares favorably with the corresponding angle (3.0°), obtained on the basis of the constants calculated by the first method.

When the standard error of estimate, which gives the degree of scatter of the points about their respective regression lines of least squares was computed for the four sets of data, the following values were found:

	Females	Males
Regression method	0.0482	0.0440
y^2–weight correction method	0.0495	0.0375

In the case of females the regression method gives a fit with the smaller scatter, while in the case of males it

gives a larger scatter, that is, a worse fit. The values of the standard error may be considered, however, as essentially of the same order of magnitude. The result, consequently, does not favor either of the methods over the other.

It was pointed out (Hersh, 1931) that for the fifteen stocks average facet number is a logarithmically damped periodic function of k, where k is determined by the y^2-weight correction method. The periodic curve very roughly approximates a damped sine curve of the general type

$$y = A\, e^{-\lambda k} (\sin nk + m) \qquad (10)$$

in which y is the difference of the average facet number with the asymptote; A, is the amplitude; λ, the logarithmic decrement; k, the coefficient of growth-partition; n, a frequency factor; and m, the initial phase.

It is to be remembered that k is a ratio of the relative growth rate of the ventral to that of the dorsal lobe. The data give no information on the actual relative rates of growth of either lobe. The ratio, k, may have a higher or lower value whether the actual relative growth rates of the lobes are high or low. The periodic curve may mean that with uniform increase in k the actual relative rates take alternately higher and then lower values, bringing about alternately higher and lower average facet number. This is perhaps what would be expected if the relative growth rates be restricted in the values which they may have by being mutually adjusted to one another and to other processes of the whole system in which the facet determination takes place. In the paper mentioned (Hersh, 1931) an interpretation of the periodic function was given in terms of growth centers and gradients of growth potential, which change from stock to stock but in some uniform manner with change in value of k.

The main point of interest at present is whether the average facet number is similarly a periodic function of κ, the coefficient of growth-partition when it is determined

by the regression method. It happens that the detection of periodic functions in empirical data is exceptionally hazardous and a conservative position would no doubt hold that the existence of periodic relationships in empirical data are to be accepted only where they are obviously suggested by the data. The periodic curve in the present instance was originally suggested by the graph of average facet number plotted semilogarithmically against k (see Hersh, 1931, fig. 9). When it was looked for in a similar graph for the males (Hersh, 1931, fig. 8) the periodicity was perhaps still indicated but not so clearly as in the case of the females.

When the average facet number is plotted semilogarithmically against κ, the points for both males and females fall within a triangular-shaped area, suggestive of a damping effect. The apical angle of this triangular area is about the same for both males and females. The apex of this triangular area for females is at the point $y = 58$ facets, $\kappa = 1.72$; and for males at $y = 80$ facets, $\kappa = 1.44$. The former are very similar to the corresponding values ($y = 57$, $k = 1.80$) for the published curve for females, while for the published curve for males no corresponding value can be given, since the damping effect is not clearly indicated.

The single points for the stocks do not follow any noticeable periodicity. The distribution is rather suggestive of a random one. A periodic curve may be drawn, however, but the critical points, the maxima and minima, are not marked by points given by the data. It is clear that in general the results of the comparison give no certain criterion for deciding which of the two methods of applying least squares to the determination of the constants of relative growth is to be preferred. It may be suggested, however, that if, in such cases with systematic variation in the genetic constitution, it is confirmed that the phenotypic quantity is a periodic function of the coefficient of growth-partition estimated by one of the methods but not for the other one, then that method

would be the preferred one, since it yields the larger number of generalizations.

Summary

In the application of the relative growth function the constants have been determined for the most part graphically. Where a high degree of genetic control makes it feasible to undertake the estimation of the differences in the constants of relative growth brought about by a relatively small genetic difference the method of least squares is clearly to be preferred. The fitting of a curve to data by this latter method may be carried out in two ways: (1) in terms of the arithmetic values of the variables x and y, and so the fit is to the equation, $y = bx^k$, or (2) in terms of the logarithmic values, in which case the fit is to the equation, $\log y = \log b + k \log x$. The first method is based on the theoretical y^2-weight correction, while the second is the familiar regression method. A comparison is made of the results obtained by applying these two methods to data on facet number in the dorsal and ventral lobes of the eye in males and females of fifteen genetically diverse stocks of bar-eyed Drosophila. The two methods give somewhat different results, but no certain criterion is established for deciding which of the two methods is to be preferred.

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A CONSIDERATION OF EVOLUTION FROM A THERMODYNAMIC VIEW-POINT[1]

DR. HAROLD F. BLUM

DIVISION OF PHYSIOLOGY, UNIVERSITY OF CALIFORNIA MEDICAL SCHOOL

PRACTICALLY since its first definite formulation by Darwin the concept of chance variation and natural selection has dominated the study of evolution, although frequent attempts have been made to replace or modify it. Probably most such attempts are provoked by a vaguely defined awareness of an insufficiency in the natural selection hypothesis, and the recognition of a directive factor in evolutionary processes which persists through successive generations. The latter concept, which is commonly known as orthogenesis, is supported by a considerable amount of evidence (*e.g.*, see Berg, 1926), but at present is not widely accepted among biologists. The general reason for abandoning or neglecting this concept has been the failure, thus far, to demonstrate the existence of the necessary directing factor outside of theological doctrine; and one may suspect that the fear of leaning too closely to such doctrine has caused most biologists to "shy off" from orthogenesis. It will be the aim of the writer to indicate the actual existence of a directing factor in evolutionary processes, while at the same time avoiding all necessity of invoking theological concepts.

Let us try first, however, to analyze the reasons for dissatisfaction with the hypothesis of natural selection as the exclusive factor in evolution. The theory of natural selection demands the assumption of inherited chance variation or mutation, with factors of the environment to remove unfit individuals; it is assumed that unfit hereditary strains would be thus eliminated. However, chance variation or mutation must mean freedom to vary in all

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directions; and therefore it would seem impossible to eliminate a given group of mutants, no matter how poorly adapted to a given environment, because these mutants must always continue to appear. This is true if statistical quantities are considered, as must be the case.

To explain this we may picture two successive mutations, form A producing an occasional mutation to form B, and B occasionally giving rise to C. For brevity we may write:

$$A \rightarrow B \rightarrow C$$

Now on the basis of chance variation we must admit that there is as great a chance for the steps to take place in the reverse order, $C \rightarrow B \rightarrow A$, and assuming that all three mutants are equally adapted to their environment we should witness an equilibrium condition which may be represented:

$$A \rightleftarrows B \rightleftarrows C$$

If we now assume that one of these mutants, C, is better adapted to the particular environment than the other two, we must expect that the number of individuals of form C will tend to increase; but even though the actual number of individuals of this type increases, neither B nor A will be completely wiped out, because both have been previously able to exist in the particular environment, and mutations in the order $C \rightarrow B \rightarrow A$ will always continue to occur. Thus, in a given unchanging environment, we can only assume that an equilibrium will exist in which the unfit individuals will continue to appear in a definite statistical ratio, although they may be destroyed soon after their appearance. Obviously, this is not the case, since evolution has definitely progressed, and certain forms have long ago ceased to appear.

However, the necessity of ruling out such an equilibrium condition may be met by assuming a changing environment. Thus, if we assume that an alteration of the environment occurs which renders the survival of B

impossible, while allowing *C* to continue to live, *A* must be permanently suppressed so long as the new environment exists. It may be pointed out that a temporary environmental change, lasting less than the lifetime of the individual, *e.g.*, a seasonal change, could not serve to eliminate *A*, even though all the *B* individuals were destroyed, for new *B* individuals would continue to appear as mutants from *C* and as soon as the environment returned to its previous condition so that *B* individuals might exist long enough to reproduce, *A* individuals would again begin to appear. The assumption that the environment as a whole has undergone major changes within evolutionary time is commonly accepted, but that this would be necessary for evolution by chance mutation and natural selection does not appear to have been emphasized. The changing environment should give direction to evolution, *i.e.*, the direction of evolution should be toward adaptation of the organism to its environment as that environment changes.

Under the above specified conditions the doctrine of natural selection may be accepted as a possible mechanism for evolution, but a difficulty arises in that too little evidence exists of the mutations which must have been produced which did not have survival value, and of those back mutations which must have occurred. Short of cataclysmic environmental changes which could have abruptly broken the chain at frequent intervals in the manner described, these mutations must have occurred in great numbers and the same ones repeatedly. It is principally the lack of evidence of such mutants in the historical record of evolution which has led paleontologists to the postulation of a directive factor in evolution.

These difficulties might be at once eliminated by assuming that mutations are irreversible, in other words, that the series of mutation steps, $A \rightarrow B \rightarrow C$, is alone possible, and that the reverse order of occurrence is impossible or at least much less probable. Thus the occurrence of *B* or any other mutant from *A* would be a matter of

chance, but the reverse mutation from *B* to *A* would be restricted. Thus, if by some change of environment all the individuals of type *A* were destroyed, individuals of this type could never again appear. This would give a definite direction to evolution, while at the same time that direction would remain entirely a matter of chance until the instant of its determination. I will point out below that such irreversibility of the direction of evolution should exist and will indicate the underlying factor for this irreversibility.

Evolution of the Environment

On reading that most interesting little volume, "The Fitness of the Environment," by Professor L. J. Henderson, one must be impressed by the close fit which exists between the organism and its environment. One is, of course, led to speculate as to the reasons for the exactness of this fit, and the way in which the organism and its environment have been molded together. As pointed out above, the concept of a changing environment is a necessary postulate for the theory of evolution by natural selection, and it would seem quite reasonable to consider the organism and the environment as mutually fitted to each other. This leads to the search for a common directive factor in the evolution of both the environment and the organism. To the writer it appears that we do not have far to seek to discover a possible directive factor, since it would seem to be provided by the second law of thermodynamics. The principle of irreversibility involved in this concept supplies the necessary irreversibility which has been shown to be required for the evolutionary process, the direction of development being such as would always be accompanied by an increase of entropy, the return over the same pathway being prohibited by the fact that it would involve a decrease in entropy.

We may examine this hypothesis more fully: For our study we may consider the earth as an isolated system,

and for such a system we may safely assume that the second law of thermodynamics holds, *i.e.*, that the entropy of the earth tends always to increase toward a maximum. The modification of the earth toward its present state must then have taken place with an increase of entropy which may be regarded as the directive agent for this change. Let us consider the evolution of the inorganic chemical compounds on the earth, assuming that this process commenced from a more or less homogeneous mixture of a given number of elements. The chemical reactions possible would be limited to those taking place with a decrease in free energy, and thus an increase in entropy.[2] The primary tendency would be to eliminate those reactions taking place with the greatest decrease in free energy, which would tend to go almost to completion. Thus we must find that most of the existing chemical compounds are the result of reactions which have taken place with a considerable decrease of free energy the probability of whose reversal would be small. An example is the reaction of hydrogen and oxygen to form water, which takes place with a decrease of free energy of about 56,000 calories per mol; we may reasonably assume that this reaction ran practically to completion at a very early stage of inorganic evolution, so that all the H_2 available was removed from the earth's surface.

We may assume, then, that there should have been produced very early a certain number of compounds with high free energies of formation; these compounds might then proceed to react together along the lines of greatest free energy decrease. If rates of chemical reactions were proportional to their free energies, the combination of chemical elements would have taken place entirely with reference to this latter value, and the earth might long ago have been a dreary and monotonous waste. Actu-

[2] Those not acquainted with the terminology of thermodynamics may, for the purpose of this paper, simply regard free energy and entropy as quantities with opposite signs but not as equivalent; free energy represents chemical potential. For a discussion of the principles of chemical thermodynamics see Lewis and Randall (1923).

ally, however, there is no direct relation between free energy and rate of reaction, and we have been permitted a more varied existence. The reactions having the greatest rates of reaction must always have taken precedence, and thus the free energy decrease should have given only the general direction to inorganic evolution, while rate of reaction should have determined its more detailed course.

An interesting case for consideration is that of ammonia, which, as Henderson (1913) has pointed out, possesses most of those properties which make water so eminently fit as a major environmental component. The formation of NH_3, like H_2O, takes place with a considerable decrease of free energy—about 3,000 calories per mol; and, since N_2, H_2 and O_2 should all have been present in large quantities in the early history of our earth, it should have been possible for large quantities of both these substances to be formed. However, the rate of formation of NH_3 from its elements is extremely slow as compared to that of H_2O, so that the formation of the latter compound would have taken precedence. This may reasonably account for the fact that the H_2 of the earth's surface was not used up in combining with N_2 instead of O_2. Thus, in one respect organic evolution on this earth was given direction very early, *i.e.*, it could only develop in a water environment, since water was the only suitable substance present. We might speculate as to the possibility of the development of life along an ammonia environment, in another solar system lacking in O_2; for NH_3 is not impossible as an environment, as Henderson seems to intimate, but prohibitively improbable in our solar system, since elementary oxygen must have been present at one time or another in all the offspring of our sun so that H_2O rather than NH_3 must have been formed. From the quantity of H_2O on our earth's surface we may reasonably assume that its formation was one of the more readily occurring reactions at an early period of our planetary development.

As stated above, the fact that rate of reaction and free energy have no direct relationship must have contributed to the complexity of the existing earth, since certain reactions must have taken precedence over others, and thus avoided the uniform exhaustion of free energy. The fact that the earth must also have been continually radiating energy into space had a limiting effect on the number of possible reactions by decreasing the incidence of those having high heats of activation. The occurrence of some reactions must have been affected by the physical properties of their resultants, *e.g.*, the formation of insoluble precipitates; thus the insolubility of silica would account for the fact that silicon does not appear as a building stone for living materials in the same manner as carbon, its near neighbor in the periodic system, whose oxides are gaseous and therefore have remained available for reactions. Another factor which must have been of great importance in delaying the process of eliminating all possible reactions was spatial separation, *i.e.*, the formation of compounds capable of reacting, but at different points on the surface of the earth. Thus today, limestone exists in many localities, although it would be rapidly attacked by moderately weak acids existing at other points of the earth. Considering these various complicating factors, one realizes that inorganic evolution must have become more and more complex. The total general direction, however, must have been always the same—toward an increase in entropy and thus toward the elimination of those reactions involving a great decrease in free energy, particularly those having high rates of reaction.

We may introduce at this point a useful analogy: If a large mound of earth were allowed to be eroded away by a constant flow of water over its surface, the water being applied just at the top of the mound, the force producing erosion would be proportional to the potential energy represented by the difference in level between the top of the mound and its base. Assuming purely me-

chanical factors, the rate of erosion would be proportional to this force. This potential may for our purposes be considered as analogous to chemical potential represented by free energy, although like all analogies this one is not exact but only useful in illustrating the general concept involved. As the mound decreased in height the potential energy would decrease in proportion and consequently the rate of erosion would proceed more and more slowly; the geologist will recognize in this analogy the principle of peneplanation. If we accept the concept that the entropy of the earth is and has been increasing, we must assume that, certainly so far as concerns chemical reactions, the rate of increase of entropy is decreasing, since those reactions taking place with the greatest decrease in free energy must have been eliminated first in this process of chemical peneplanation.

It might be objected that this analogy is false in that, as previously mentioned, rates of chemical reactions are not proportional to the free energies of the reactions concerned. However, given a great period of time such as has undoubtedly elapsed since the formation of our earth, most reactions would have had time to occur, given the proximity of reacting substances and the proper conditions. Thus, although the particular reactions occurring may have been selected according to their rates, the general tendency would be to eliminate first those reactions taking place with the greatest decrease in free energy. In the case of the analogy of erosion, the rate is not only determined by the potential energy represented by the height of the mound, but also by the refractoriness of the soil to erosion. The soil not being homogeneous, the rate of erosion might be expected to proceed more rapidly at some points of the mound than at others, resulting in the formation of channels in which the water would be directed; and having thus relieved the harder parts of the action of the eroding agent the tendency would be to increase the difference in rate of erosion between the hard and the soft parts. Thus, although we might be

unable to predict where the channel would form, once formed it would tend to maintain itself rather than to seek new channels. Of course, if there were a stone visible in the mass of soil, we might predict that the soil would be eroded first rather than the stone, although we might not be able to predict exactly the course of the channel. In the same way we might have been able, given the opportunity, to have predicted that the formation of H_2O from H_2 and O_2 would have been one of the earlier reactions to occur in the development of our earth, but the subtler channels which the degradation of chemical energy might pursue we should have had great difficulty in foreseeing. However, we might have felt certain that in whatever channel started, the tendency would be to maintain that channel simply because of the impossibility of going back over the path commenced. This appears to be implicit in the principle of irreversibility involved in the second law of thermodynamics.

Considering all these factors, we should expect that to-day there are a less number of possible reactions involving large decrease in free energy than at any previous time. Those which remain exist because they have low rates of reaction, because of peculiarities of the reactants concerned or of spatial isolation. The majority of reactions which remain should be those involving small free energy changes and therefore enjoying a high degree of reversibility, depending upon the concentrations of the reactants. The more recent evolution of chemical compounds has, of course, been greatly modified by biological activity, as will be pointed out below.

THE EVOLUTION OF LIVING SYSTEMS

It would seem reasonable to assume that the above outlined principles apply to the development of living systems as well as non-living, and the writer will attempt to point out the manner in which they may have directed organic evolution. Let us assume that in the course of the progression toward a condition of greater entropy,

systems were formed in which certain reactions could reproduce themselves over and over again. We need not concern ourselves here with the time or manner of origin of these systems, although we must admit the possibility of their being formed by the chance combination of chemical reactions. These would, of course, represent the ancestor systems of our existing living organisms. In such recurring systems we must admit the existence of cycles in which reactions taking place with increase in free energy were coupled with reactions taking place with a greater decrease in free energy, the total cycle always resulting in a loss of total free energy. Such a system would be analogous to a hoop rolling down an incline; if we consider a given small section of the hoop, during one phase of its revolution this section will undergo an increase in potential energy, but during the alternate phase it will undergo a greater decrease in potential energy, so that the total result is a loss in potential energy. Such systems find their parallel to-day in the autotrophic bacteria which depend for their existence upon the degradation of chemical energy. These bacteria, whose chemistry has been reviewed by Baas-Becking and Parks (1927) are capable of utilizing certain inorganic reactions taking place with loss of free energy to drive the cycle of the living organism. As they point out, the efficiency of these organisms in the utilization of this potential energy is not high, and there is no reason to consider them as essentially different from other physico-chemical systems.

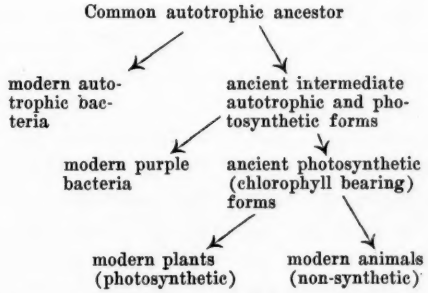
Obviously, such systems may exist only so long as a supply of the particular chemical compounds is available for the reactions which furnish the potential energy, and with the exhaustion of the supply of these compounds the systems perish. It is quite possible that the earliest ancestral forms may have disappeared coincidently with the exhaustion of certain chemical compounds in the process of inorganic evolution; but in the course of the existence of these ancestral forms mutants may have

appeared which could utilize other reactions for driving the cycle, and these in turn have existed until the supply of the proper reactants disappeared. While it is possible that mutants might have appeared having a greater increase in free energy during the upward phase of the cycle than that of the parent forms, mutants having a smaller corresponding change in free energy would be more probable, since they could be driven by reactions involving a correspondingly smaller decrease in free energy, and certainly large free energy changes would be possible only in the latter direction. Let us assume a series of possible mutations, $A \rightarrow B \rightarrow C$, in which the free energy changes involved in the upward phase of the energy cycle have the relationship $A > B > C$. The greater the free energy changes involved, the less will be the reversibility of the chain, and if A or B disappeared as a result of any environmental change there would be very little or no chance of its reappearing. Thus an irreversibility should exist such as was pointed out as essential for a hypothesis of evolution by chance variation and natural selection, which would provide a directing force in organic evolution.

Another step must have occurred early in evolutionary time; the introduction of photosynthesis, a mechanism whereby radiant energy from the sun could be set to producing reactions taking place with an increase in free energy. Since in photochemical reactions the energy is added directly to the molecule, the formal second law of thermodynamics does not apply, since this law is derived from consideration of statistical numbers of molecules. Photosynthesis must have greatly influenced the course of evolution, but could not affect the general tendency toward increase in entropy, *i.e.*, the photosynthetic reaction furnishes a supply of compounds which can furnish energy for reactions taking place with an increase of entropy. The effect may be compared to a geological model similar to that used above: The sun provides

energy for transforming water into the vapor state, which water is subsequently precipitated as rain onto a mountain which it erodes. The potential energy for this is provided by the sun, but the course of erosion is directed by gravitation which tends always to diminish potential mechanical energy. Likewise, the energy for most of the living processes we know is provided by the sun through the mechanism of photosynthesis, but the direction of these processes follows the second law of thermodynamics, *i.e.*, the direction is toward a decrease in chemical potential or free energy. We may point out that at present the photosynthetic process is tending to decrease the entropy of the earth through the transformation of radiant energy into chemical potential, and we may well wonder how closely this comes to balancing the increase of entropy. The question is, of course, unanswerable at present, but we may justly assume that the two magnitudes are closer together to-day than in the past.

The probability that the photosynthetic process developed from systems like the autotrophic bacteria is given support by the existence to-day of forms which are perhaps intermediate; *e.g.*, the purple bacteria (see Van Niel, 1930). We might diagram the relationship thus:



We have here shown the modern non-synthetic animals as an offshoot from former photosynthetic forms. This seems a reasonable development when we consider that

porphyrins, the complex organic substances from which chlorophylls are built, are quite universally distributed throughout the animal kingdom, *e.g.*, in hemoglobin and in cytochrome, and also that the chromosome system is common to both. This may also account for such forms as Euglena, which have both animal and plant characteristics.

In our scheme, we have indicated that the modern forms have diverged from the ancient, the ancient having gone permanently out of existence. This is in accordance with the principle of irreversibility outlined above; were any of the ancient forms in existence to-day we might expect them to mutate in the direction of the existing forms and we should see the entire process of evolution going on before our eyes, which is distinctly not the case. We must assume that the common ancestors have completely disappeared, and that mutation back to these forms is prevented by the irreversibility of the mutation process; this does not mean, of course, that a great many forms have not been in existence for a very long time. Thus we can only expect divergence, and the persistence along certain lines of divergence even to extinction, but we could not have predicted the direction of this divergence had we been given the opportunity. We might assume that many other pathways might have been followed had there been a start made in these directions; having failed this, however, evolution can never occur along these pathways, but must continue in the lines it has commenced.

More complex systems. We have thus far considered living organisms as undifferentiated systems in which certain primary chemical reactions take place. This treatment is probably entirely justified for the early ancestral forms of the existing organisms, and probably for existing simple forms such as the autotrophic bacteria. However, there may be some question as to whether the higher forms in which the reproductive mechanism responsible for mutational changes has been so distinctly

differentiated from the remainder of the organism may be so considered. To trace the development from a simple asexual system, such as I have postulated, to the highly developed existing sexual forms would be an impossible task; but we may attempt to apply the concepts I have discussed to modern highly developed forms having a gene type of inheritance, and if the same principles seem to apply we may reasonably assume that they have functioned in the development of these more complex forms from their simpler ancestors.

We may assume that the gene type of inheritance was introduced at a quite early date, at which time the control of reproduction had been transferred to some special part of the cell, to be later transferred to particular cells in the more highly developed organisms. The direction of evolution from this time on must have had its point of determination in these specialized parts, the rest of the organism having little or no direct place in this process so that environmental changes could have little or no effect on the direction of mutations. However, the principles outlined above should still be applicable to the gene system; *i.e.*, a mutation involving a genic change must be more probable in the direction of a decrease in free energy of the gene complex than in the opposite direction. Thus there must have been a direction to evolution in that a line of development once established would involve a certain degree of irreversibility.

It is commonly assumed that mutations are not appearing as rapidly at present as in past time, and thus that the process of evolution is slowing down. This is, of course, what we might expect; for, as previously stated, the rate of decrease in free energy must be diminishing, and as a general rule the reactions taking place with the greatest free energy should have been already exhausted. In the case of mutations, we must assume that those taking place with greatest loss of free energy should have occurred first and, their precursors being eliminated, can no longer occur. This should apply to the processes

within the chromosome as well as to others, since actual changes within genes or rearrangement of genes within the chromosome must take place with some change in entropy, although in the latter this may be insignificant. The greater the increase in entropy involved in a given mutation the greater must be the irreversibility of the process, and the greater the probability of its occurrence, so that those mutations involving great increase in entropy have probably already occurred for the most part. Thus we might expect that changes within genes would be much less frequent at present than mechanical rearrangement of genes.

It is impossible to know at exactly what point we stand on the curve of the increase of entropy, but if the slope of the curve is less than at any previous time we should expect that the rate of occurrence of great mutations is much less than at previous times, although lesser mutations might be even more frequent. It may be that we are actually at a point on the curve of entropy increase where the slope is very small and that most of the mutations occurring to-day represent very small changes in free energy, and thus enjoy a high degree of reversibility; such mutations would not persist long. This actually seems to be the case, since the incidence of persisting mutation would appear to be small at the present time.

We might discuss numerous other factors which have affected evolution which are to a certain extent explainable on the basis of the irreversibility of chemical reactions, as for example, a constant internal environment. Similarly, we might make application of the same general principles to embryology and through this to the biogenetic law. The writer hopes to be able to discuss some of these questions in the near future.

In all this process natural selection must have played an important part; in fact, the persistence of a form must always depend upon its ability to cope with its environment, no matter how that form may have been produced. The present thesis is thus not at all antagonistic to the

concept of natural selection, although perhaps requiring some modifications of that concept. On the other hand, the thesis does afford an explanation of the general evidence for a persistent direction in evolution in that it provides an actual directive factor. At any rate, we must recognize the constant irreversible changes which occur in our world as a factor in organic evolution.

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SHORTER ARTICLES AND DISCUSSION

THE BROWN VARIATION AND GROWTH OF THE HOUSE MOUSE[1]

THE probable evolutionary significance of the types of variations which are characteristically mendelian factors is important to the further advance of the subject. The writer has during the past six years devoted considerable time to an analysis of some of the typical mendelian factors of the house mouse, Norway rat and several races of the deer mouse, with a view toward a more thorough evaluation of these as foundations for the process of evolution of the rodent forms. The brown variation of *Mus musculus* is one which was used at an early stage of the work. The usual consideration of this and similar variations as modifiers of the pigmentation only is an entirely superficial attitude. To students of mammalian genetics mention of the dominant yellow allelomorph of agouti and the dominant white spotting factor which is also lethal when homozygous in house mice will sufficiently impress the point. To apply the Darwinian theory to such variations with reference to the modification of color only is to admit many errors. The brown variation of the house mouse may be quite insignificant in evolution, for example, because of the color change, yet of considerable importance because of other physiological alterations which it induces in the individuals which possess it. With the exception of the feathered predators of mice vision does not appear to equal the value of smell and hearing in the search for prey. The predatory birds are probably all devoid of color vision. Present information indicates that the various shades of darkness possible in a mouse's color are all well within their range of vision. Further, there is not sufficient evidence to indicate that a selection would be made by them between color types on the basis of the amount of light absorption, even though the background became less concealing.

The brown variation of the house mouse is not one of the most striking in the degree to which it appears to modify the constitution of the mouse. The normal black pigmentation is prevented by this recessive mendelian character from reaching a full stage

[1] A contribution from the Laboratory of Vertebrate Genetics of the University of Michigan.

of development, probably an oxidation. The pigment of the eye protects a brown animal far less effectively from strong light than the darker pigment of black mice protects them. Sunlight fades the brown fur more than the black. Growth in terms of body-weight was the first criterion of physiological constitution used in the study of the brown and other variations. This complex character was compared in brown and black mice which were litter mates. The use of such animals excludes several sources of error in the measurements. The work reported here is incomplete and compares homozygous brown with heterozygous black mice. It is regretted that similar data are not yet available on a series of the constitutions *bb*, *Bb* and *BB*. The homozygous black animals were not used because of the lack of cages for the adequate testing of their constitution. Data on certain other characters provide some reason to expect differences between the homozygous and heterozygous black types.

The effects of the character upon mice of three different stocks was observed. A rather small race, a considerably larger race and the first cross-bred generation from these two were used. The small race was derived from the introduction of brown into a wild caught strain of house mice. The observations recorded in this paper were made on members of a single line after five generations of brother-sister matings. Both brown and black were in this stock, but no other common variation was present. All individuals were thus either black or brown white-bellied agouti. The large race was derived from a stock of laboratory house mice secured from the Bussey Institution colony through the kindness of Doctors W. E. Castle and C. E. Keeler. This stock was black and tan, an agouti allelomorph, and carried both black and brown. The mice used in this study were from a single line following three generations of brother-sister matings. Reciprocal matings between these two stocks produced the third group of mice. It was composed of both black and brown animals, which, as would be expected, showed no other variations, although they were all heterozygous for black and tan.

Uniformity of environmental conditions surrounding the development of the mice which were studied was provided for in every manner possible. A commercial dog food with supplementary rations was uniformly provided in adequate quantities. Weaning, caging and other features of the handling of the experimental animals were not changed during the work. Females

TABLE I

COMPARATIVE GROWTH OF BLACK AND BROWN HOUSE MICE

No.	Race	Sex	Type	Mean weight in grams					
				31st day	61st day	91st day	121st day	151st day	181st day
41	5 H	♂♂	Bb	9.1 ± .14	15.6 ± .19	17.9 ± .22	19.5 ± .25	22.4 ± .26	22.8 ± .27
45	5 H	♂♂	bb	9.3 ± .14	16.0 ± .20	18.3 ± .21	21.0 ± .24	23.0 ± .26	23.6 ± .31
47	5 H	♀♀	Bb	8.4 ± .13	14.3 ± .14	15.4 ± .15	17.7 ± .17	19.1 ± .16	20.0 ± .19
44	5 H	♀♀	bb	8.6 ± .13	14.5 ± .14	15.7 ± .15	18.2 ± .18	19.8 ± .22	20.8 ± .24
38	3 J	♂♂	Bb	9.8 ± .14	19.5 ± .28	23.0 ± .28	25.7 ± .31	28.2 ± .26	30.4 ± .24
35	3 J	♂♂	bb	10.1 ± .15	20.0 ± .30	23.6 ± .25	26.4 ± .30	29.0 ± .27	32.1 ± .24
39	3 J	♀♀	Bb	9.1 ± .14	17.0 ± .19	21.3 ± .17	24.0 ± .22	25.4 ± .17	29.0 ± .19
36	3 J	♀♀	bb	9.4 ± .13	17.4 ± .16	21.6 ± .21	24.5 ± .24	25.8 ± .18	29.7 ± .26
50	1 HJ	♂♂	Bb	9.5 ± .15	17.8 ± .17	19.9 ± .21	22.4 ± .24	24.1 ± .17	25.9 ± .19
46	1 HJ	♂♂	bb	9.8 ± .15	18.2 ± .18	20.2 ± .25	22.8 ± .21	24.6 ± .19	26.6 ± .20
47	1 HJ	♀♀	Bb	8.8 ± .15	16.4 ± .16	17.7 ± .19	20.5 ± .23	22.0 ± .16	23.8 ± .19
50	1 HJ	♀♀	bb	9.1 ± .16	16.7 ± .16	18.0 ± .19	20.9 ± .17	22.5 ± .17	24.5 ± .19

were separated from males at the age of 21 days and no pregnancies occurred in the animals weighed. By these efforts several causes of variability of growth were eliminated, although numerous external factors undoubtedly operated which increased the variability of this very complex character.

An examination of the results of the weighing of the mice at several ages which are recorded in Table 1 permit certain conclusions in regard to the comparative growth of black mice heterozygous for the brown variation and of mice homozygous for brown. Since it is improbable that these mice differed genetically in other respects it is safe to assume that any differences which appeared between the two classes of individuals are probably due to the effects of the brown gene. The data indicate quite clearly that quantitative differences in body size accompany differences of constitution for the brown gene. The homozygous mice appear larger at all ages at which the mice were weighed. Their larger size becomes increasingly obvious as age advances. Brown males were 3.9 per cent. heavier than black males and brown females were 3.1 per cent. heavier than black females as adults. The individuals of the several genetic stocks show parallel differences, which greatly supports the view that it is the brown gene which is responsible for the larger size and not other genetic factors which may accompany it by genetic linkage or other means.

The work of Green (1931a, 1931b and 1933) on the hybridization of *Mus musculus* and the similar but distinct, smaller *M. bactrianus* has provided valuable data upon the brown-black, non-agouti-agouti and dilute-intense pairs of characters. He made a large number of records on body weight as well as on other size characters. His data on the back-cross generation obtained by mating the hybrids back to the triple recessive house mouse parent are of interest in this connection. The fact that a cross between species was involved probably does not alter the value of the data on the comparative growth rate of brown and black mice. Green observed that brown mice are significantly larger than comparable black animals at most stages of development. His weighings started at earlier ages than those recorded in this paper and indicate that the black mouse heterozygous for brown is heavier than the brown on the first and eleventh days of life, but after the thirty-first day the reverse obtains. His data therefore agree with those reported in this paper. The

mice which he compared were derived from back-crossing the hybrids between a small black race and a larger brown race with the latter. This fact caused Green to ascribe the larger size of the brown mice to a linkage of the brown gene with a factor or factors for large size from the brown race. It appears more logical to ascribe the larger size of brown individuals to the action of the gene itself, for in the case of the mice studied and reported upon in this paper it is not possible to trace a linkage or coupling of the brown gene with large-size factors. Certainly it is impossible to ascribe it to a linkage as loose as Green (1935) calculates for his material. Crossing over would have separated the brown factor from the large size if a linkage that loose existed in my material.

The general conclusion to be derived from the data presented in this paper is that the brown variation of the house mouse causes certain physiological changes in addition to a color change. Brown mice grow more rapidly than black ones. Since body weight is a composite result of the operation of numerous physiological factors it appears reasonable to assume that the change or changes wrought by this character are fundamental in nature. Where metabolic rate or its product growth is a factor of survival, the brown variation would prove of value, either positive or negative. Since brown is recessive to black it is not safe to assume that all recessive genes are deleterious.

HORACE W. FELDMAN

BOSTON, MASS.

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TEXT-BOOK FACTS ON PROTECTIVE COLORATION

TEXT-BOOKS mold the views of students—of some for a temporary period, of others for life. It is desirable, therefore, that they include a minimum of questionable material. The compilers, however, feel an obligation to summarize all knowledge in a given field, and especially to reflect recent advances. The task is difficult, and if held to a high standard of accuracy, perhaps impossible. As an illustration of how some things get into text-

books, and why they should come out, the following history is submitted.

Among assertions in the crowning work of two authors, both producers of numerous text-books, is the following:

> Protective or cryptic coloration is certainly very common but its life-saving value should be proved, not simply assumed. Not every case is so satisfactorily documented as that of the green Praying Mantis on the green herbage, and the brown variety among the withered leaves. For in this case the protective value has been proved up to the hilt and statistically measured.[1]

The quotation avers that "Not every case is so satisfactorily documented," but the documentation consists of one page of text accompanied by two graphs.[2] The "proved to the hilt and statistically measured" encomiums are lavished upon wholly uncritical experiments by a vacationing student which dealt with 110 specimens. The student himself says, "It will of course be necessary to repeat the experiments upon a larger scale." He did not repeat the experiments, but another investigator[3] did and obtained divergent results.

The first experimenter, in describing his investigation, states, "The form chosen was *Mantis religiosa,* which occurs in Italy (where the experiments were made) in two forms, a green and a brown. It is interesting to notice that the green form is always found upon green grass, the brown form upon grass burnt by the sun" (p. 58).

The last sentence serves notice of the uncritical character of the performance, for on its face it does not seem probable. For instance, the common native mantid (*Stagmomantis carolina*) of the eastern United States has a green and a brown phase, but these show no preference for harmonizing backgrounds, according to the observations of long-experienced collectors. Referring to *Mantis religiosa* itself, a scientist writing[4] of experience in France says that there is nothing to indicate that the mantids seek a background of their own color (p. 9). There are, furthermore, color forms intermediate between the green and brown, so that the second experimenter worked with three, namely, green, yellow and brown.

[1] J. Arthur Thomson and Patrick Geddes, "Life: Outlines of General Biology," I, pp. 417–418, 1931.

[2] A. P. Di Cesnola, *Biometrika,* III: 58, 2 figs. (graphs), 1904.

[3] M. M. Beljajeff, *Biol. Zentralbl.,* 47 (2): 107–113, 2 figs. (graphs), 1927.

[4] Etienne Rabaud, *Bul. Biol. France et Belgique* 67 (1): 1–69, 1923.

In brief, the first experiment and its results were as follows: 20 green individuals exposed (tied) on green herbage and 20 brown on brown herbage were untouched by enemies in 17 days; while 25 green on brown were all killed in 11 days, and of 45 brown on green only 10 were left after 16 days of exposure, when a storm terminated the experiment. "Of the individuals which died," the author says, "nearly all were killed by birds; but of the 25 green individuals exposed on brown grass, five were killed by ants" (p. 58).

It is apparent that this experimenter (No. I) made no preliminary survey of the site to learn what possible enemies of mantids were present, and that in the end he did not really know what killed the mantids. Experimenter II insists that "the experimental field should lie in a known hunting territory of some certain kind of bird" and that "the field must be under observation during the whole of the experiment" (p. 112).

The French critic previously referred to cites Judd's trials with insects harmonizing almost perfectly with the background. These are sufficiently summarized in the following quotation.[5]

> I put several admirably protected grasshoppers (Acrididae) among the fallen brown oak leaves, where I found them with the greatest difficulty, in a cage with a song sparrow, a junco, and white-throated sparrows. The legs of the insects had been pulled off, so they kept perfectly still, but the birds instantly saw and seized the grasshoppers. I tried the same experiment in a large cage with mockingbirds and got the same results (p. 468).

Pointing to these results Rabaud says:

> Di Cesnola did not take the same care; he exposed mantids on harmonious or contrasting backgrounds, without ascertaining whether the birds ate mantids, or whether they ate them habitually or exceptionally; he did not place certain birds in the presence of the mantids, but simply exposed the latter to the attacks of predators of all kinds. Under these conditions the experiment does not reply to the question posed, is not worthy of consideration.
>
> Moreover birds are not the sole enemies of mantids. Divers hymenoptera, family Sphegidae, pursue and capture them to the exclusion of other prey. With these predators, sight does not play more than a secondary rôle. Perhaps they appreciate shape; certainly they appreciate odor more than color (p. 14).

This latter remark surely applies to ants, which Experimenter I admits killed 5 mantids; they may have killed others and the total, whatever it was from this cause, would have no bearing on the question of protective coloration.

[5] Sylvester D. Judd, AMER. NAT., 33: 390, 461–484, June, 1899.

Experimenter II made two studies. In the first he used green, yellow and brown forms of *Mantis religiosa,* of which the brown were indistinguishable and the other two groups sharply distinct from the background. In 14 days there were removed by birds (wheatears, kestrels) from 20 of each kind exposed, 12 yellow, 11 green and 4 brown, percentages of 60, 55 and 20, respectively. In his second study, out of 26 of each color used, there were taken by rooks and kestrels in 24 hours, 12 yellow, 11 green and 12 brown mantids (p. 110). He notes that the first result is in accordance, the second not to be brought in accord, with the selection theory, and further remarks:

> As is known there has been great controversy as to whether the Darwinian "natural selection" or chance controls the destruction of living creatures in nature. My experiments appear to show as a consequence of differing conditions (intensity and character of the selection, biological peculiarities of the selecting factors, etc.) that one as well as the other can occur (p. 112).

This experimenter mapped the position of the mantids eaten, and they were so clearly taken from adjacent positions and by groups as to suggest that choice was affected by ease of capture from certain perches used by the birds—an element of chance that apparently was not taken into consideration.

As Experimenter II intimates, what we really wish to know are the actual occurrences in nature. Experiments are not likely to produce the desired knowledge, but we certainly are justified in drawing conclusions from available information on the color phases of the mantids in nature.

Despite what Di Cesnola says, we must accept as nearer the truth Rabaud's conclusion that the mantids do not seek a background of their own color. The variability in coloration alone is sufficient evidence that the insects would find discovery of harmonious surroundings impracticable. Not only the variability, but the continued existence of the color phases, and their occurrence in single broods, show that they do not have great practical importance for the mantids. Rabaud informs us that pairing proceeds without regard to color.

If selection of the color phases for harmony with background were a reality, as theory, Experimenter I and the text-books assert, one or another of the phases would long ago have been "selected" as standard for the species. They would not have continued to be manifested together in pairs, and in broods, in which, regardless of the character of the background, one of the

pair, or a certain proportion of the brood, could not possibly be "protected."

Rabaud concludes "from the point of view of offense as well as that of defense, the mantid does not gain any evident advantage from its coloration. One should not forget that the term 'green' or the term 'brown' designate only the most divergent phases of color, . . . that the clear green mantid lives at a season when concolorous foliage is not plentiful, and the opportunity of playing the rôle of homochromy is seldom realized. The chances of realization are not more frequent for the brown mantids and for the same reason: the homochromy of *Mantis religiosa* pertains to the realm of legend" (p. 15).

This is quite a different way of referring to the worth of protective coloration in *Mantis religiosa* from the "proved to the hilt" assertion of the text-book, but one, if we must choose between extremes, that according to the evidence presented is perhaps the more acceptable.

Some one has said that the theories of to-day are the text-book facts of to-morrow, but that dictum fails in the very necessary admission that many theories never attain the status of facts. In so stating we have in mind the popular use of the term "fact," for dependable information. There is a meaning with dictionary sanction, however, that may be more consoling to the makers of text-books and that is—anything alleged.

W. L. McATEE

BIOLOGICAL SURVEY, WASHINGTON, D. C.

THE INHERITANCE OF YELLOW-PIGMENTED HEADS IN DOMESTIC FOWL

IN the fall of 1931 two Barred Plymouth Rock pullets were noticed in the farm flock with yellow pigmented heads, including the comb, wattles, ear-lobes and face. In the spring of 1932 these pullets, together with other hens, were mated to a Rock male, the progeny from which were intended to be inbred.

From the two yellow-head pullets, 11 males and 13 females were obtained, none of which had yellow heads. In 1933 an F_1 mating was made which resulted in 18 yellow and 35 non-yellow males and 9 yellow and 22 non-yellow females. The proportion of non-yellows to yellows is thus approximately 2:1 in the males and 2.4:1 in the females, the combined proportion being 2.1:1.

A further test was made in 1934 by mating a yellow male to yellow females. Since this was the second generation of inbreeding, only a few individuals were obtained, owing to poor hatchability. The numbers obtained were 15 males and 14 females, all of which were yellow. In this group, however, two males at 8 weeks of age and two females at sexual maturity, all from the same mating, had head furnishings with considerable reddish color, but were unmistakably yellows. The same yellow male was also outcrossed with Barred Plymouth Rock and White Leghorn females, giving in all 47 progeny, none of which had yellow heads.

The results indicate that the yellow-head characteristics are inherited as a simple recessive to the usual red-head condition, and non-sex-linked. The proportion of yellows to non-yellows in the F_2, especially among the males, is a poor fit for a 3:1 ratio. However, the number of individuals is small, and when the two sexes are combined the excess of yellows to non-yellows on the basis of a 3:1 ratio is only six.

The characteristics of yellow-pigmented heads is readily distinguished and can be observed in chicks of a few weeks of age. The shade of yellow is somewhat paler and not so bright in the immature birds as that found in the shanks of yellow-shanked birds. The males retain the yellow-colored heads until approaching sexual maturity, at which time the head furnishings take on an orange and later an orange-red appearance. During the winter months most of the pigment disappears, except in the blade of the comb which, together with a paler color of head furnishings, makes it just possible to distinguish the yellow from non-yellow males. The head furnishings of the females at sexual maturity likewise turn an orange color, with frequently a pinkish or reddish tinge to the comb serrations, ear lobes and wattles. They do not, however, turn reddish to the same extent as the males. After a period of laying, most of the yellow pigment gradually disappears in a similar manner to that in the shanks and beak, which results in pinkish, pale-colored heads, by which they can always be readily distinguished. In addition to the deposits of pigment the yellow-head factor would thus seem to affect the vascularization of head furnishings, particularly of females. Bright, red combs are regarded as an indication of birds being in good laying condition, which would seem to be substantiated by the fact that compared with a similarly inbred group having a common male ancestor, the yellow-heads

are very poor layers. Our data, however, are too limited to draw definite conclusions on this score.

Several experiments have been conducted on the inheritance of yellow pigmentation of beak, skin and shank color in domestic fowl. Thus Bateson and Saunders (1902) found that crosses between white and yellow shank colored breeds gave an F_1 with whitish shanks, and when these were bred inter se white, whitish and yellow shank colored birds appeared. Later Hurst (1905) and Dunn (1925) confirmed the observations of Bateson and Saunders with larger numbers and found white shank color to be dominant, or almost completely dominant, to yellow shanks. Dunn used the symbol W for white and w for yellow. The gene W is regarded as inhibiting the yellow or lipochrome pigmentation of the shank and is non-sex-linked. Lambert and Knox (1927) crossed white- and yellow-skinned birds and found skin color to be inherited similarly to shank color. These authors suggested that yellow beak, skin and shank color were correlated, and retained the same symbols as used for shank color.

The yellow-head characteristic is doubtless dependent for its expression upon the yellow skin factor, found in Rocks, Leghorns and many other breeds. Thus yellow-skinned birds with red-head furnishings could be thought of as having a dominant factor which inhibits the yellow pigmentation of the head or restricts the pigment to the beak, skin and shanks, the mutation of which has given rise to the yellow heads. The symbols I or R would therefore be appropriate, as would Y for yellow, but these symbols are already in use and since it is desirable to use single letters when possible, appropriate symbols would be GG (Gelb) for non-yellow heads and gg for yellow heads.

ALAN DEAKIN
GEORGE ROBERTSON

CENTRAL EXPERIMENTAL FARM
OTTAWA, ONT.

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AN EXPERIMENT ON A RELEASED POPULATION OF *D. MELANOGASTER*

A POPULATION of *D. melanogaster,* which is not endemic in England, and most probably absent from the area, was released at Dartington Hall, Totnes, South Devon. The population of 36,000 individuals had the following constitution—1Eb.Eb: 2Ebeb: 1eb.eb. At the end of the summer, some 120 days after the release, the frequency of the gene ebony obtained from the genetic analysis of all the Wild Type flies trapped was now $.11 \pm .03$, having fallen from .5 in about 5 to 6 generations. The values of the frequency of ebony obtained from the different parts of the estate, including a foodstore, did not differ significantly from the value $.11 \pm .03$ for the whole of the trapped population. The intensity of selection was greater than if all recessives had been eliminated in each generation, and this raises the issue of selection of the heterozygote.

CECIL GORDON

DEPARTMENT OF ZOOLOGY,
UNIVERSITY COLLEGE, LONDON

AN ANALYSIS OF TWO WILD DROSOPHILA POPULATIONS

IN order to obtain a rough estimate of the frequency of recessive genes in wild populations a number of wild females of *Drosophila melanogaster* and *D. subobscura* were caught at one station in southern England. All or nearly all the flies had already been fertilized. None showed any heritable abnormality. The F_1 progeny were allowed to mate together, and usually 8 F_2 families were bred.

In most F_2 series recessive genes appear in about one quarter of the families, thus making it probable that the F_1 is derived from a single male.

In 1933, 13 Melanogaster families yielded 5 genes. One is an allelomorph in the ebony series, one is a new and more intense allelomorph of cinnabar, and one a new occurrence or a new allelomorph of rotated abdomen, while two are undescribed. Eleven Subobscura families gave three genes which are under investigation, and three which are lost. All genes found in this year were autosomal recessives.

In 1934 I was more experienced in detecting mutants, and the yield was far greater. Ten families of Melanogaster yielded 9 certain and 2 doubtful genes. About 5 of these genes are distinct autosomal recessives. One is a sex-linked recessive for short cross vein.

Sixteen families of Subobscura yielded 21 autosomal recessives, 3 doubtful genes and one probably sex-linked recessive. Fourteen of these are certainly distinct, one (for short veins) has repeatedly appeared.

Thirty-five families of Melanogaster and 81 of Subobscura were grown as far as the F_1 only, but no further sex-linked genes were detected, although 2 Subobscura families may have shown some sort of lethals.

Subobscura is thus at least as rich in recessives as Melanogaster. Tschetverikov (1927) and Dubinin and his colleagues (1934) found no sex-linked recessives in wild populations. I found with Timofeeff-Ressovsky (1927) that they do occur, though much more rarely than autosomals. However, their expression is very slight and no dominants or definitely sex-linked lethals were found as by Timofeeff-Ressovsky. It appears that the probability of finding an autosomal recessive detectable by my methods of examination in an individual wild Drosophila is rather over half.

Clearly just as x-rays furnish the best method of obtaining new sex-linked genes, inbreeding furnishes the best method of obtaining new autosomal recessives.

The genes found in Melanogaster are now being located and a linkage in Subobscura has already been found. The Subobscura genes include some analogous to eyeless, shaven, rough eye, outstretched, shortened vein forms and a few eye colors in Melanogaster. Some show effects not described in Melanogaster.

CECIL GORDON

DEPARTMENT OF ZOOLOGY
UNIVERSITY COLLEGE, LONDON

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CHROMOSOME ALTERATION IN CREPIS

ALTERATIONS in chromosome numbers, due to the duplication of a single chromosome or an entire haploid genom, are well-known phenomena in *Crepis,* as in many other plants. A condition less frequently found is that in which fragmentation or translocation, or a combination of both, occur, producing a new chromosome number. Two plants of *C. sibirica* have been found in which such a change occurs in one of the chromosomes bearing a satellite, the D-chromosome. These plants were both taken from a single culture. A third plant from the same culture showed the normal genom for this species.

The root-tips were taken from the plant in the rosette stage and fixed in chromacetic formalin, using the formula given by Hollingshead and Babcock (1930) as solution I.

The chromosomes of *C. sibirica* consist of five pairs, in one of which the members bear small satellites (Fig. 1). The satellited chromosomes are only ones having a small proximal arm.

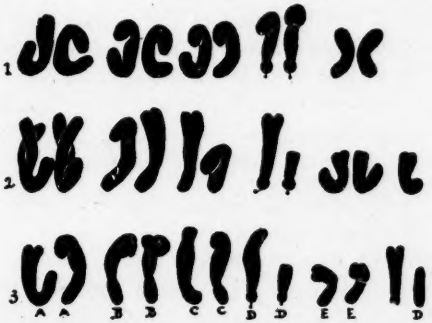

FIG. 1. Chromosomes of normal genom of *Crepis sibirica.* Fig. 2. Genom from plant with one satellited chromosome fragmented, and forming an extra chromosome. Fig. 3. Genom from cell with two extra chromosomes. Figures were drawn from material sectioned at ten microns and stained in iron hematoxylin, with Leitz 1/12 oil immersion objective and Leitz periplane oculars.

In the two plants showing variations from this normal grouping, two chromosomes were found which were smaller than any found in the normal genom, with a count of 11 chromosomes. When these are arranged in pairs (Fig. 2), it is found that one satellited chromosome was very short, about one half to two thirds of the length of the other satellited chromosome. There

was no change in the proximal arm or in the satellite. The extra chromosome was somewhat longer than the small satellited chromosome, though shorter than any other one in the group. Its constriction was difficult to locate definitely, but the proximal arm seemed to be slightly longer than that of the satellited chromosome. The combined length of these two short chromosomes in most cases seemed to be about equal to that of the normal satellited chromosome, though occasionally the total length was greater than the length of the satellited chromosome in the same cell.

There seems to be no doubt that these two small chromosomes together represent the second satellited chromosome of the normal genom. Eleven chromosomes were present in all the cells of the root-tips from these two plants (10 from one plant, 7 from the other), with a few exceptions. A few cells showed a duplication of one chromosome. In the cell shown in Figure 3, this seemed to be a duplication of the satellited chromosome, though somewhat shorter in length.

The method of the formation of the spindle fiber attachment for this new chromosome affords a matter for speculation only, as there are no evidences as to its origin.

OLIVE SWEZY

UNIVERSITY OF CALIFORNIA
BERKELEY

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